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An energy budget for a woodland population of oribatid mites

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With 14 figures

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Contents

1. Introduction

The energy budget of a population can be expressed, using the notation recommended by the International Biological Programme (Petrusewicz & Macfadyen 1970), as:

$$C = A + FU$$
$$A = P + R$$

where C equals consumption; A equals assimilation; FU equals rejecta; P equals production and R represents the energy used in respiration or cost of maintenance.

There have been several attempts to quantify these relationships for invertebrates (e. g. Saito 1967, Wasilewska 1974), but the information for field populations of oribatid mites is scant. Since the pioneer work of Engelmann (1961) much of the emphasis has been placed on the estimation of individual parameters (e. g. Berthet 1964, Kowal & Crossley 1971, McBrayer & Reichle 1971). A further approach has been the elucidation of the energy budget for a laboratory population of a single species, e. g. *Steganacarus magnus* (Nicolet) (Webb & Elmes 1972); *Carabodes labyrinthicus* (Michael) [Steigen, Solhoy & Gyllenberg 1975]. Luxton (1972, 1975) has summarised much of the known data on the nutritional biology, calorimetry and respirometry of oribatid mites.

In the present study field densities, biomass, age-structure, faeces production, assimilation rate, respiration and methods of estimating production have been investigated in an attempt to derive an energy budget for a woodland population of oribatid mites. Where information is lacking, or considered inadequate, then data from the literature have been used in an effort to increase the accuracy of each parameter studied.

2. Site and sampling procedure

2.1. The sample site

The population study of soil and litter dwelling Oribatei was carried out at Meathop Wood, a mixed deciduous woodland 29.83 hectares in area lying 3.2 kilometres east of Grange-over-Sands, Cumbria, England. The woodland is situated on Meathop Fell, an isolated outcrop of carboniferous limestone, 13.7 metres above sea-level.

All soils within the sampling site are naturally freely drained. Two soil types predominate, Rendzinas on the scarp edges and pavements, and Brown earths overlying limestone associated with the drift of the terraces.

The woodland vegetation consists largely of oak *Quercus* spp.; ash *Fraxinus excelsior* LINNAEUS; birch *Betula pendula* ROTH and *B. pubescens* EHRHART, with patches of yew *Taxus baccata* LINNAEUS. The dominant trees are 15.2 to 18.3 metres high. The understorey is generally well formed and locally dense. It includes hazel *Corylus avellana* LINNAEUS; hawthorn *Crataegus monogyna* JACQUIN; spindle *Euonymus europaeus* LINNAEUS and buckthorn *Rhamnus catharticus* LINNAEUS. The ground flora is dominated by *Mercurialis perennis* LINNAEUS; *Rubus fruticosus* LINNAEUS and *Brachypodium sylvaticum* BEAUVOIS.

The mean monthly soil temperatures at 0 cm. and total rainfall for each month of the investigation are illustrated in Fig. 1a and b.

2.2. The sampling procedure

Thirty sampling statinos, each of one square metre, were evenly distributed within the one hectare study plot. The sampler used to obtain soil cores was based on that described by MACFADYEN (1961). Fifteen samples of 1/250 m^{-2} and 6 cm deep were taken each month within the period August 1967 to July 1969. Each permanent sampling station was therefore visited six times in each year of the investigation. Each sample was divided horizontally into two halves and extracted using an apparatus based on the High Gradient Cylinder Extractor (MACFADYEN 1961).

3. Population density and age-structure

3.1. General remarks

Five species: *Nothrus silvestris* NICOLET; *Platynothrus peltifer* (C. L. KOCH); *Hermannia gibba* (C. L. KOCH); *Parachipteria punctata* (NICOLET) and *Tectocepheus velatus* (MICHAEL) were selected for age-structure analysis because of the relatively high numbers of both adult and immature stages. The less abundant representatives in the samples were either recorded as species e. g. *Steganacarus magnus* and *Steganacarus striculus* (C. L. KOCH), or as species-groups e. g. *Oppia-Suctobelba* sp., *Nanhermannia* sp. and "other oribatids".

3.2. Nothrus silvestris

The seasonal variations in population density at Meathop Wood are given in Fig. 2a. Peaks of abundance were recorded in August and from February to May. These observations are comparable to those made by WEEB (1970). Spring peaks of abundance have also been recorded by GASDORF & GOODNIGHT (1963) for a population of *Nothrus* sp. and by MORITZ (1963) and LEBRUN (1965) for *N. silvestris*. These authors record an additional peak of density between October and December.

The monthly changes in the abundance of each life-stage of *N. silvestris* are shown in Fig. 4. Adults were examined for eggs between January and December 1968, (Table 1). Gravid individuals were present throughout this period with the maximum mean number of eggs per adult being observed in May (3. 25). Relatively large numbers were also recorded in January (2.54). All the developmental stages of *N. silvestris* were represented in each month's samples. Peaks of larval abundance were observed in the August/September and February/April periods of the year with an additional peak in December of 1968. The periods of larval influx into the population coincide with or follow those times when the adults contain high numbers of eggs. The peaks of nymphal and adult abundance coincide with those of the overall population density of this species. Consequently at Meathop Wood there is no observable transition through the successive developmental stages of *N. silvestris*. WEBB (1970), studying this species from a Danish heathland soil, records a high incidence of immature stages during February/March which developed rapidly to produce breeding adults between April and June. Eggs laid during this time hatch to produce larvae in August which

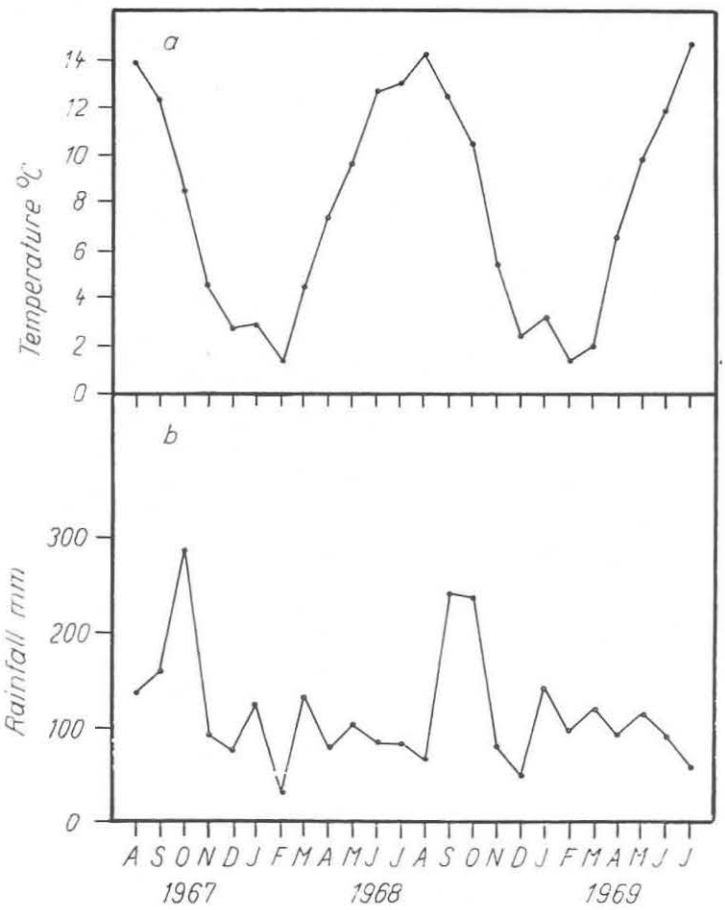

Fig. 1a and b. Climatic data: (a) Mean monthly soil temperature (°C) at 0 cm. (b) Monthly rainfal (mm).

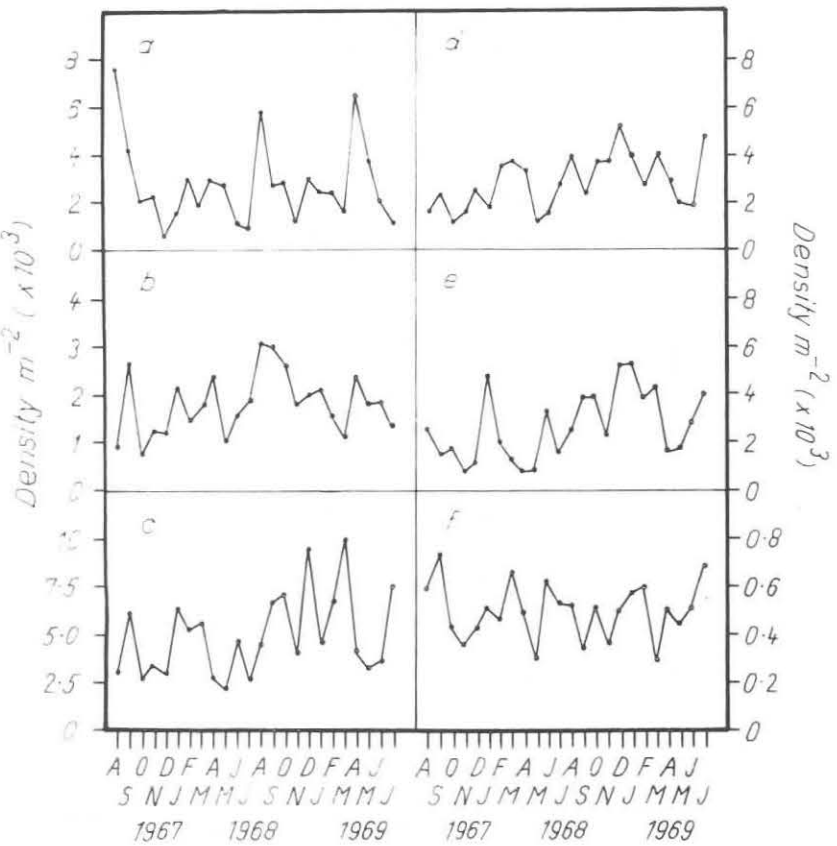

Fig. 2a–f. Monthly population density data. (a) *Nothrus silvestris*. (b) *Platynothrus peltifer*; (c) *Tectocepheus velatus*; (d) *Hermannia gibba*; (e) *Parachipteria punctata*; (f) *Steganacarus magnus*.

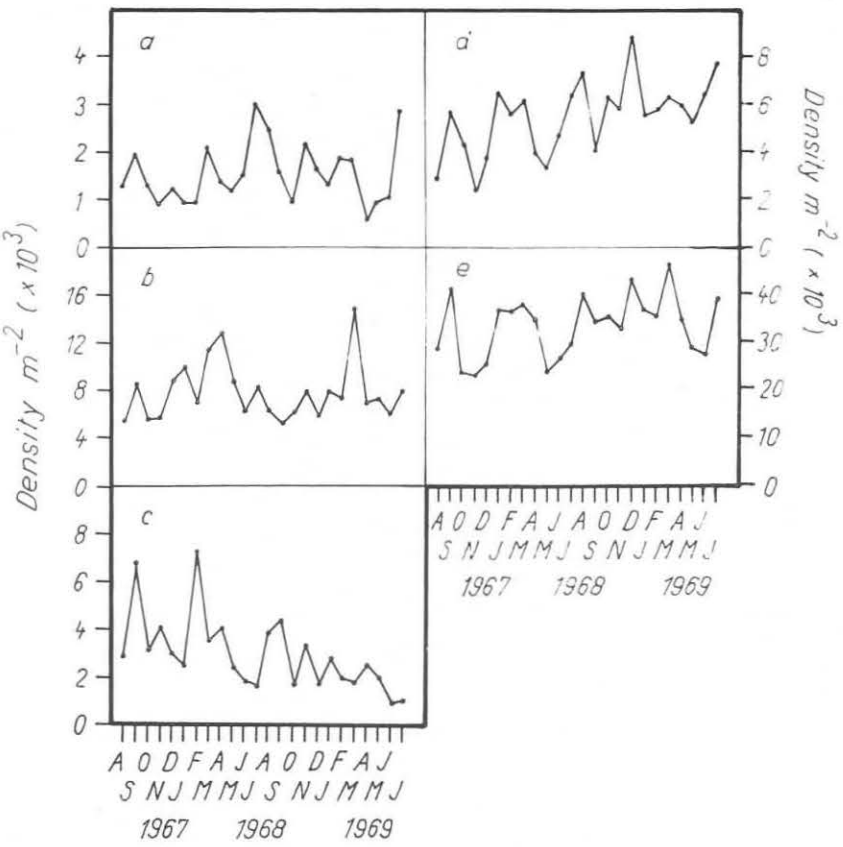

Fig. 3a—e. Monthly population density data: (a) *Steganacarus striculus;* (b) *Oppia-Suctobelba* sp.; (c) *Nanhermannia* sp.; (d) "other oribatids"; (e) total Oribatei.

Table 1. Mean number of eggs carried by each adult

Date	Species		
	Nothrus silvestris (gravis adult)	*Platynothrus peltifer* (gravid adult)	*Hermannia gibba* (gravid female)
1967			
August			1.90
September			0.12
October			—
November			0.25
December			1.25
1968			
January	2.54	—	2.25
February	1.43	—	3.64
March	1.71	0.21	3.52
April	1.17	5.64	5.47
May	3.25	8.80	6.67
June	2.33	8.00	5.32
July	2.25	4.80	3.20
August	0.60	1.38	1.90
September	1.78	0.05	0.13
October	1.97	—	—
November	1.50	—	0.67
December	1.92	—	1.14
1969			
January		0.09	2.40
February		0.05	3.50
March		0.08	2.91
April		3.63	5.42
May		8.13	5.17
June		8.86	3.33
July		4.74	3.50

— indicates no eggs carried.

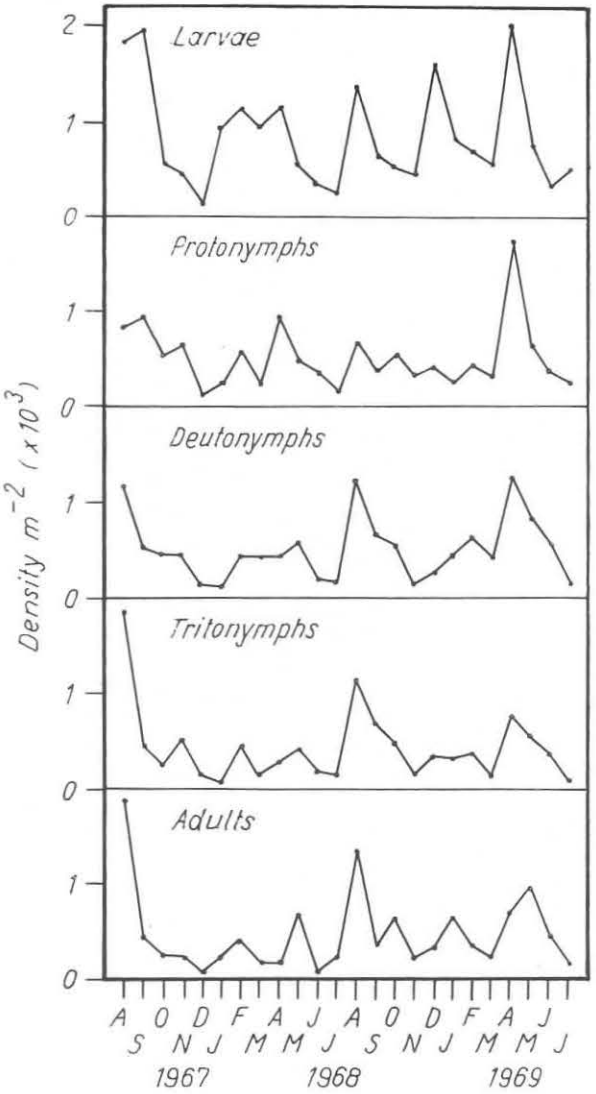

Fig. 4. Monthly density data for each juvenile and the adult stage of *Nothrus silvestris*.

then pass through the successive nymphal stages to produce breeding adults in December. The age-structure data of the present study and that of WEBB (1970), together with the population density changes recorded by GASDORF & GOODNIGHT (1963), MORITZ (1963) and LEBRUN (1965), indicate that *N. silvestris* initiates two generations a year.

3.3. Platynothrus peltifer

The seasonal variations in population density of *P. peltifer* are given in Fig. 2b and show an August/September maximum with a subsidiary peak in April. These observations agree closely with those of HARDING (1973) for *P. peltifer* from a broad-leaved forest site, and are similar to those of HAARLØV (1960) for this species from the soils of a Danish hawthorn thicket. USHER (1975) records a single population maximum during the spring (March to May). However, BLOCK (1966) recorded peaks in June from both sites investigated with additional peaks in December and January from the limestone grassland site.

The seasonal changes in the abundance of each developmental stage of *P. peltifer* at Meathop Wood are given in Fig. 5. Adults were examined for eggs between January 1968 and July 1969 (Table 1). Gravid adults were present in the population from January to September. The maximum mean number of eggs per adult was recorded in May 1968 (8.80) and June 1969 (8.86). Larvae were present from July to December with a peak of abundance in the August/September period. Protonymphs were recorded between July and April with two peaks of abundance in the first year of the investigation (September and January) and

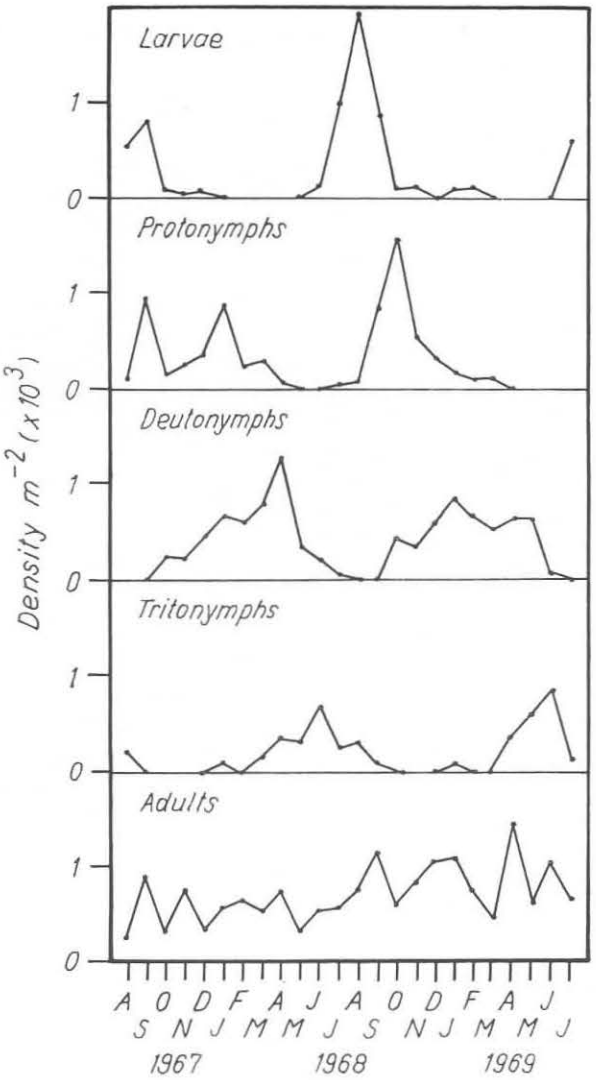

Fig. 5. Monthly density data for each juvenile and the adult stage of *Platynothrus peltifer*.

a single peak (October) in the second year. Deutonymphs were present from October to July with a peak in April 1968 and January 1969. Tritonymphs were recorded from January to September with a peak of abundance occurring in June of both years of the study. The adult stage was recorded throughout the period with high numbers present in the September samples. An additional peak of adult abundance was observed in April 1969. These observations on the phenology of *P. peltifer* from Meathop Wood are similar to those of HAARLØV (1960), BLOCK (1966), HARDING (1973) and USHER (1975).

The main egg-laying period at Meathop Wood occurs from April to July. These eggs hatch to produce the August/September peak of larvae. The protonymphs and deutonymphs, the main immature overwintering stages, rapidly develop in the spring to produce the early summer peak of tritonymphs. The transition to adults is not clear because of the continual presence of this stage in the population. However, the timing of tritonymphal peaks together with the September high of adults suggests that this transition takes place in the summer months. HAARLØV (1960) suggests that oviposition occurs shortly after adult emergence. This is supported to some extent by HARDING (1973) for *P. peltifer* of the Ercall, a wooded hillside in Shropshire. However he concludes that adults emerging from mid-August onwards fail to produce eggs until the following year. At Meathop Wood the occurrence of gravid adults prior to the main period of tritonymphal-adult transition seems to preclude the possibility that many adults produce eggs in the year that they themselves develop, consequently they overwinter and lay eggs the following spring and early summer.

3.4. Tectocepheus velatus

The monthly changes in the abundance of *T. velatus* are shown in Fig. 2c. Population density peaks were observed in the December/January and September/October periods, with an additional peak in March of 1969. MURPHY & JALIL (1964) found two density maxima in November and March. USHER (1975) also records two maximum population densities occurring in October/November and again in May. LEBRUN (1965) observed one peak of metabolic activity in August for *T. velatus* from Belgian forest soils. BLOCK (1966) recorded February/March and September density peaks for this species from a limestone grassland site, but only one from peat soils (August to December). REEVES (1969) studying *T. velatus* from four cover sites recorded density peaks in April, August and November. The published data therefore shows that this species has at least two density maxima, but the precise timing of these peaks differs between the sites investigated.

The seasonal changes in the abundance of each life-stage of *T. velatus* from Meathop Wood are given in Fig. 6. Larvae were present throughout the sampling period, with the exception of April 1968, and two peaks of abundance were recorded in February and July. Protonymphs were only absent from the July 1968 samples and density peaks of this stage occurred in September and December/January There is a suggestion of a third protonymphal peak in March. Deutonymphs and tritonymphs were recorded throughout the study period. Peaks of deutonymph abundance were found in March with a relatively high incidence between September and January. Tritonymphal peaks of density were recorded in September/October, June/July with additional peaks in February 1968, December 1968

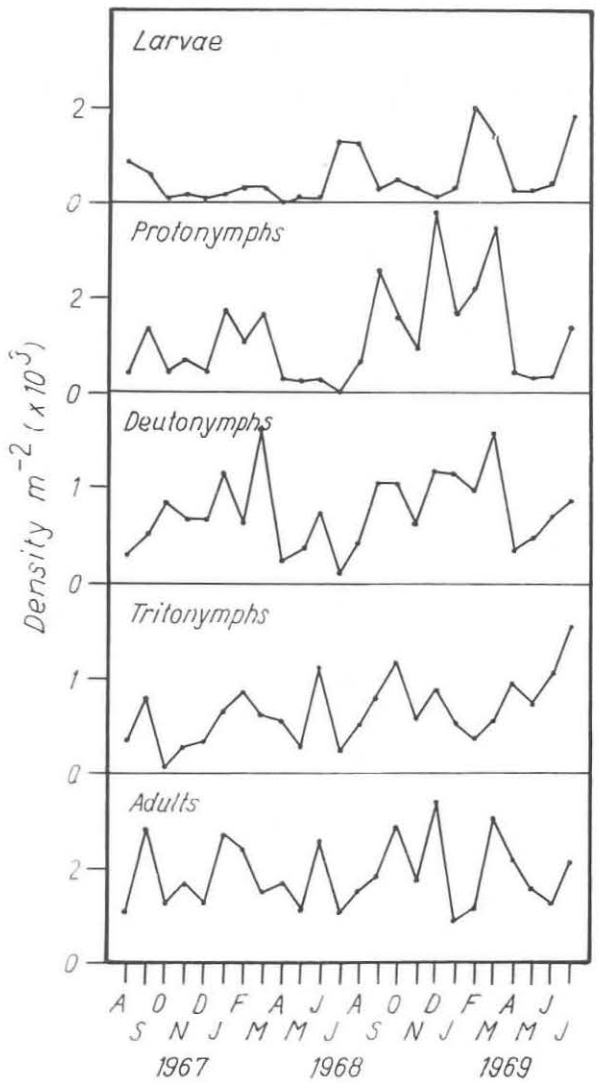

Fig. 6. Monthly density data for each juvenile and the adult stage of *Tectocepheus velatus*.

and April 1969. Peaks of adult abundance were recorded in September/October, January/February 1968, December 1968 and March 1969. The age-structure data for *T. velatus* from Meathop Wood does not show any clearly defined transition through successive developmental stages, but the presence of two larval peaks indicates that two generations a year are initiated. This conclusion is supported by HAARLØV (1960) and MURPHY & JALIL (1964). However LEBRUN (1964) attributes 3—5 generations a year to *T. velatus*, and WALLWORK (1967) suggests that a similar number of generations could occur when the environment conditions are favourable.

3.5. Hermannia gibba

The seasonal variations in population density of *H. gibba* are given in Fig. 2d. Peaks of abundance were recorded in August/September and March with an additional peak in December 1968. EVANS et al. (1961) observed peaks of abundance for this species in February and November. BÄUMLER (1970) recorded high numbers between October/December and in May 1968. However the significance of the May peak is doubtful as *H. gibba* was at a low density at this time the previous year.

The monthly changes in the abundance of each developmental stage of this species at Meathop Wood are shown in Fig. 7. Adults were examined for eggs between August 1967 and July 1969 (Table 1). The sex of the adults could be determined by measuring the length

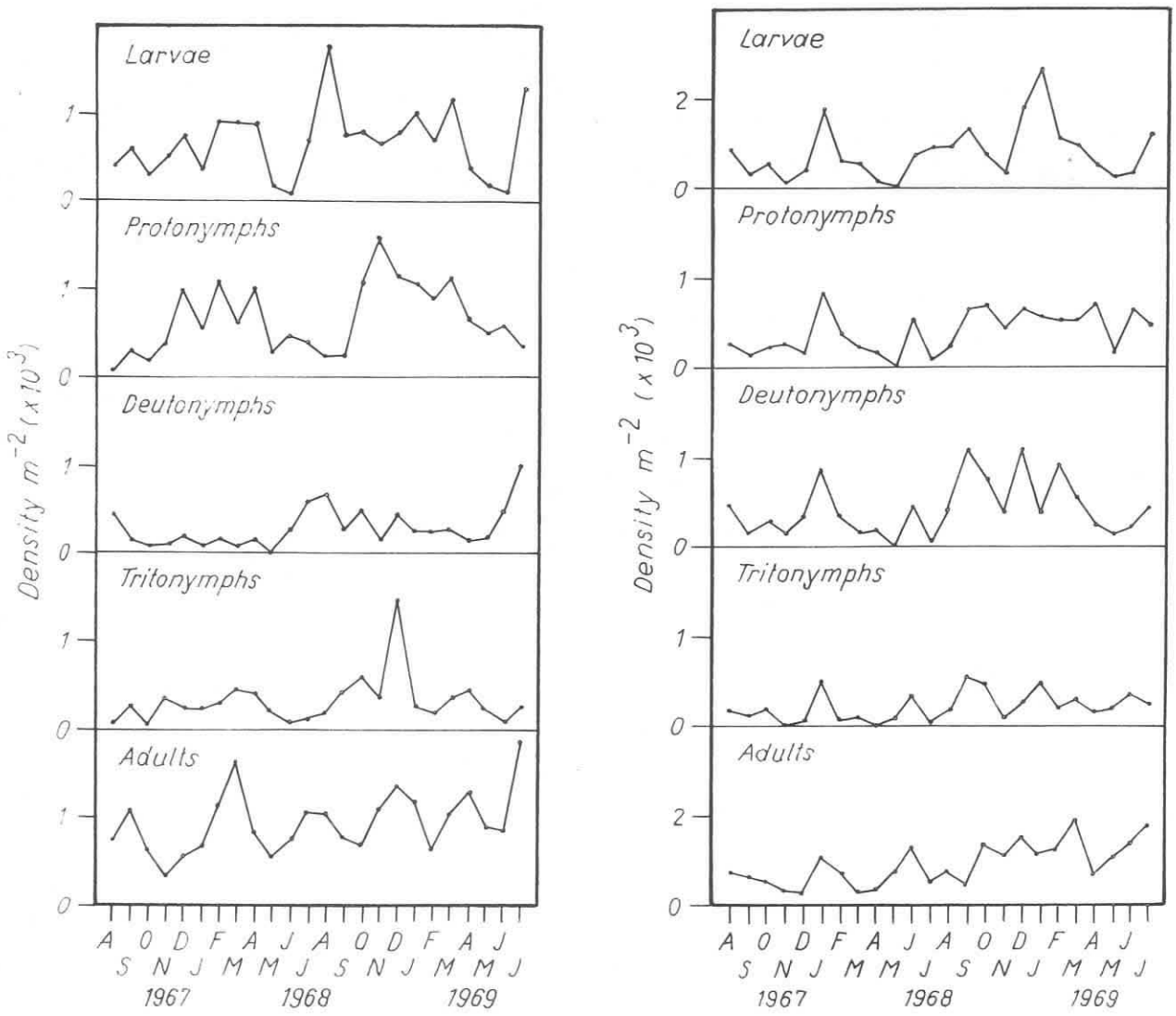

Fig. 7. Monthly density data for each juvenile and the adult stage of *Hermannia gibba*.

Fig. 8. Monthly density data for each juvenile and the adult stage of *Parachipteria punctata*.

of the genital plate which in females is 61.3 ± 1.61 μm (± S. E.) and in males 53.1 ± 1.78 μm (± S. E.). Gravid females were found throughout the study period with the exception of October of both years. The maximum mean number of eggs per female was recorded in May 1968 (6.67) and April 1969 (5.42). Larvae and protonymphs were present throughout the sampling period. Peaks of larval abundance were recorded in August/September and between January and April. Peaks of protonymphal abundance were observed in February and November 1968, but a generally high incidence of this life-stage was recorded between October and April. The deutonymphs were absent only from the May 1968 samples, peaks of abundance being recorded in the July to September period. Tritonymphal peaks of abundance were observed in March and December 1968. The adult stage was recorded throughout the study period but their peaks of abundance varied from year to year.

At Meathop Wood the egg laying of this species is prolonged with the main period occurring between April and June. These eggs hatch to produce the August/September peak of larvae. The continual larval influx into the population and the slow development to and from the protonymphal stage during the autumn and winter results in an accumulation of both stages during this period. Development during the spring was more rapid, giving rise to the summer peak of deutonymphs. Development continued, to produce the high incidence of tritonymphs in the winter and spring of the following year. The tritonymphal/adult transition is not clear but presumably occurs during the spring/summer months. The age-structure data therefore indicates that one generation is initiated each year and that development from the egg to adult takes approximately two years with at least a further twelve months passed in the adult stage. This conclusion is supported by Evans et al. (1961) studying this species from litter and soil under Sitka spruce. Bäulmer (1970) also gives age-structure data for *H. gibba*. However the density peaks of each developmental stage recorded by this author often coincide with the overall population density of this species. Consequently no observable transition through the successive developmental stages can be discerned from his study.

3.6. Parachipteria punctata

The monthly changes in population density are given in Fig. 2e. Density maxima were recorded in January with a secondary peak during the June to December period. No published density data are known for *P. punctata*, but Lebrun (1965) records a density peak in August for the related species *Parachipteria willmani* (van der Hammen). Haarløv (1970), studying *Achipteria coleoptrata* (Linnaeus), observed density peaks in April/May and November.

The monthly changes in the abundance of each life-stage of *P. punctata* from Meathop Wood are shown in Fig. 8. Peaks of larval abundance were recorded at those times of the year when the overall population density for this species was at a maximum. Similar trends were also observed for each of the nymphal and adult stages. Consequently no developmental transition can be deduced from changes in the age-structure composition. However the presence of two larval peaks indicates that *P. punctata* initiates two generations a year at Meathop Wood. Similar conclusions were drawn by Lebrun (1964) studying *P. willmani*. Haarløv (1960) concludes that *A. coleoptrata* initiates one generation a year, despite his observation that this species had two peaks of larval abundance occurring in the August/September and February/May periods of the year.

3.7. Steganacarus magnus

Maximum population densities of this species were recorded in September 1967 and July 1969, with a further peak occurring during the January/March period (Fig. 2f). However, statistically there are no true seasonal changes in density and the results are largely indicative of adult numbers as the immature stages were rarely present in the monthly samples. Lebrun (1965) in the litter layer only records density peaks for this species in May, October and January, whereas Usher (1975) observed an apparent winter minimum with maxima

occurring in the spring and late summer. LEBRUN (1964) attributes 2 generations a year to *S. magnus*. However, the lack of seasonal trends together with the evidence of WEBB & ELMES (1973) that the mean number of eggs and prelarvae per female is greatest in September suggests that only one generation a year is initiated by this species at Meathop Wood.

3.8. Steganacarus striculus

The seasonal variations in the population density of this species at Meathop Wood are given in Fig. 3a. Density maxima were recorded in July with further peaks in February/March and November 1968. The significance of the November peak is doubtful, as this species was at a minimum at this time the previous year. The immature stages of *S. striculus* were rarely present in the monthly samples. MORITZ (1963) studying this species from mixed woodland records two peaks of population density in the March to May and August/September periods of the year. ALICATA et al. (1973) observed peaks of density in December/January and in June for a related species, *Steganacarus brevipilus* (BERLESE). Based upon population density changes alone it appears that *S. striculus* initiates two generations a year at Meathop Wood.

3.9. Oppia-Suctobelba sp.

Monthly changes in the population density of this species-group are given in Fig. 3b. Maximum population densities were recorded during the March/April period with subsidiary peaks in September 1967, January 1968 and November 1968. BLOCK (1966) observed an April/May maxima with further peaks in the October/December and August/September periods for this species-group from mineral soils. He records peaks of density in January, March, June and October/November for this group from peat soils of mixed moor. Three peaks of population density were recorded in January, March/May and October by LEBRUN (1965) for *Oppia quadricarinata* (MICHAEL), *Oppia subpectinata* (OUDEMANS) and *Suctobelba subtrigona* (OUDEMANS). He found two peaks for *Oppia ornata* (OUDEMANS) (February and October) and *Oppia nova* (OUDEMANS) and *Suctobelba trigona* (MICHAEL), March and June/July. The seasonal changes in the abundance of each life-stage of *Oppia nova* and *O. subpectinata* given by REEVES (1969) indicate that both species are capable of rapid development particularly during the summer months and that at least two generations a year were initiated. LEBRUN (1964) attributes 2 or 3 generations a year to four species of *Oppia* and two species of *Suctobelba*.

3.10. Nanhermannia sp.

Population density peaks for this species-group were recorded in September of both years with an additional peak in February of 1968 (Fig. 3c). No major peak of density was recorded in the spring of 1969. BLOCK (1966) records maximum density in July with a secondary peak in March for *Nanhermannia nana* (NICOLET) from a limestone grassland site, with density maxima varying between July and October and the suggestion of a subsidiary peak in February for this species from peat soils. USHER (1975) found a September/October maximum for *N. nana* with a further peak in April. Both MORITZ (1963) and BERTHET (1964) record two peaks of density for *Nanhermannia elegantula* BERLESE which occur in the September/October and April to June periods of the year. The published density data for *N. nana* and *N. elegantula* suggests that both species initiate two generations a year.

3.11. Total Oribatei

The total population density of oribatid mites fluctuated between 22,866 and 40,033 m^{-2} (mean 30,324 m^{-2}) in the first year of the study and between 27,017 and 45,732 m^{-2} (mean 35,667 m^{-2}) in year 2. These values are similar to those given by DUNGER (1968) (mean 23,100 m^{-2}), MCBRAYER & REICHLE (after PETERSEN in prep.) (mean 37,200 m^{-2}) and GIST et al. (1975) (mean 55,600 m^{-2}) for oribatids of temperate deciduous forests. Considerably

higher mean population densities have been recorded by several authors including HARDING (1969) (mean 110,600 m^{-2}) and LEBRUN (1971) (mean 117,200 m^{-2}) for oak forests, and MITCHEL (1977) (mean 122,900 m^{-2}) for an Aspen woodland.

Little consistency was observed between years at Meathop Wood in the timing of absolute maximum and minimum total population density. However two main periods of high density. However two main periods of high density were recorded in August/September and in March; minimum densities were observed in November and between May/June. The periods of high density were often characterised by the presence in the population of large numbers of larvae. Similar observations linking density maxima with high larval presence have been recorded by MADGE (1965) in an oak woodland, LUXTON (1967) in a Welsh saltmarsh and HARDING (1969) for certain oribatids of an oak woodland.

4. Estimation of biomass

4.1. Prefatory note

In production biology studies it is necessary to convert density to biomass and therefore a series of weight determinations for the adult and immatures are required. Indirect methods such as those employed by VAN DER DRIFT (1951) and MACFADYEN (1952) have now been superseded by the use of accurate microbalances.

4.2. Methods

All live and dry weights were obtained using an E. M. B. 1 RIIC electromicrobalance. Prior to dry weight determination animals were placed in a desiccator containing calcium chloride at room temperature (20—22 °C) for a period of seven days. After this time repeated weighings showed no additional water loss. Whenever possible single specimens were weighed but occasionally bulking of up to thirty individuals was necessary because of their small size and a mean weight recorded. In order to estimate the biomass for a species-group, all individuals of that group were collected

Table 2. Live and dry weights ($\mu g \pm$ S. E.) of Oribatei from Meathop Wood

Species or species-group	Life stage	Live weight	Dry weight
Nothrus silvestris	Adult	56.5 ± 1.40	26.3 ± 0.73
	Tritonymph	34.0 ± 0.80	18.2 ± 0.96
	Deutonymph	15.2 ± 0.51	8.5 ± 0.65
	Protonymph	7.6 ± 0.62	4.2 ± 0.18
	Larva	4.9 ± 0.28	2.6 ± 0.20
Platynothrus peltifer	Adult	59.8 ± 1.49	27.2 ± 0.80
	Tritonymph	37.2 ± 1.07	13.3 ± 1.14
	Deutonymph	14.5 ± 1.17	6.2 ± 0.53
	Protonymph	8.5 ± 0.37	3.8 ± 0.20
	Larva	2.8 ± 0.10	1.0 ± 0.25
Hermannia gibba	Adult male	172.0 ± 2.17	69.7 ± 2.80
	Adult female	207.0 ± 8.03	88.4 ± 1.94
	Tritonymph	100.5 ± 7.19	53.5 ± 2.56
	Deutonymph	44.0 ± 2.34	20.3 ± 1.12
	Protonymph	17.6 ± 0.82	7.4 ± 0.78
	Larva	7.6 ± 0.65	2.1 ± 0.38
Tectocepheus velatus	Adult	3.6	0.98
Parachipteria punctata	Adult	33.5 ± 2.68	18.2 ± 1.02
Steganacarus magnus	Adult	270.4 ± 40.85	132.60 ± 12.12
Steganacarus striculus	Adult	No record	8.0 ± 0.36
Nanhermannia elegantula	Adult	No record	11.5 ± 0.59
Ceratoppia bipilis	Adult	63.6 ± 2.35	24.8 ± 1.57
Nothrus palustris C. L. KOCH	Adult	235.0	83.6
Hermanniella granulata (NICOLET)	Adult	No record	42.1 ± 1.89
Odontocepheus elongatus (MICHAEL)	Adult	No record	18.4 ± 1.60
Xenillus tegeocranus (HERMANN)	Adult	No record	65.1 ± 4.04
Oppia-Suctobelba spp.	All stages	No record	0.55 ± 0.13
Nanhermannia spp.	All stages	No record	6.07
"other oribatids"	All stages	No record	5.70

(where only three replicates were obtained no standard errors were calculated).

from a single month's samples, dried and weighed. This was repeated for three monthly sampling occasions within the first year of the study and an overall individual mean dry weight calculated for each species-group.

4.3. General remarks

The live and dry weights obtained for the oribatid mites of Meathop Wood are given in Table 2. The live weights are broadly comparable with those of the published data with a few exceptions. The live weight of male (172 μg) and female (207 μg) *H. gibba* is much higher than that of 70.0 μg quoted by BERTHET (1963) and 94.2 μg by LEBRUN (1971). The mean live weight for adult *S. magnus* (270.4 μg) is an intermediate figure lying within the range of values quoted by WEBB & ELMES (1972), WOOD & LAWTON (1973) and LUXTON (1975). No attempt was made in this study to differentiate between sexes and reproductive status in this species.

There has been a distinct lack of comprehensive dry weight data of oribatid mites in the literature with the exception of those of BLOCK (1966) and LUXTON (1975). In those species where all instar classes were considered, the percentage water loss on drying ranged from 44.1 % for the deutonymphs of *N. silvestris* to 72.4 % for the larva of *H. gibba*. This is within the range quoted by LUXTON (1975) and comparable to that recorded by BLOCK (1966).

Immature dry weights were expressed as a percentage of adult dry weight to ascertain whether there were any similarities between species (Table 3). No truly consistent relationship was observed and fairly large variations seen e. g. *H. gibba* larva (2.7 %) compared to

Table 3. The immature dry weights of *N. silvestris*, *P. peltifer* and *H. gibba* expressed as a percentage of adult dry weight

Species	Tritonymph	Deutonymph	Protonymph	Larva
Nothrus silvestris	69.2	32.3	16.0	9.9
Platynothrus peltifer	48.9	22.8	13.9	3.7
Hermannia gibba	67.6	25.6	9.4	2.7
Mean for the three species	61.9	26.9	13.1	5.4

N. silvestris larva (9.9 %). The results given by LUXTON (1975) show similar trends but his overall mean values for deutonymphs (25.2 %), protonymphs (12.8 %) and larvae (5.3 %) are similar to those of the present study. However the tritonymphal value of 49.0 % is appreciably lower. Nevertheless, until more accurate measurements are obtained it is considered worthwhile to use these approximations to predict immature dry weight from that of the adult. The dry weights of each of the immature stages of *T. velatus* and *P. punctata* were calculated in this manner.

4.4. Monthly biomass

The mean monthly biomass for each species and species-group in each year of the study is given in Table 4. The maximum and minimum monthly biomass estimates are summarised in Table 5.

The major contributors to mean monthly biomass were *H. gibba* and *S. magnus*, representing together 53.5 % of the total. The minor contributors were *T. velatus* and members of the *Oppia-Suctobeloa* group which collectively added 2.3 % to the overall mean monthly biomass. The mean monthly biomass increased from year 1 to year 2 of the study. The increase of 61.77 mg dwt m^{-2} was mainly attributable to the increase in biomass of *H. gibba*, a rise that represented 53.8 % of the overall rise.

Table 5 shows that the timing of absolute maximum and minimum monthly biomass was not consistent from one year to the next. The exception to this is *Oppia-Suctobella* sp. Maximum population densities often coincide with maximum monthly biomass. Certain exceptions do occur e. g. *P. peltifer* (August 1968). Although the density of this species was at a maximum at this time, the monthly biomass maximum was not recorded until April

Table 4. Mean monthly biomass (mg dwt m^{-2}) for each species and species-group for each year of the investigation

Species or species group	Year 1	Year 2
Nothrus silvestris	25.79	31.62
Platynothrus peltifer	20.33	29.79
Hermannia gibba	83.04	116.25
Tectocepheus velatus	2.30	2.86
Parachipteria punctata	15.28	29.06
Steganacarus magnus	66.06	63.10
Steganacarus striculus	11.61	12.46
Oppia-Suctobelba spp.	4.50	4.13
Nanhermannia spp.	21.75	14.05
"other oribatids"	25.96	35.07
Total Oribatei	276.62	338.39

Table 5. Period of maximum and minimum biomass (mg dwt m^{-2})

Species	Year 1 (August 1967 to July 1968)		Year 2 (August 1968 to July 1969)	
	Maximum	Minimum	Maximum	Minimum
Nothrus silvestris	101.0 August	7.3 December	73.3 August	8.5 July
Platynothrus peltifer	31.6 April	9.0 August	47.8 April	16.5 March
Hermannia gibba	154.4 March	50.3 Novemb.	200.7 December	72.7 February
Tectocepheus velatus	3.6 Septemb.	1.3 July	4.7 December	1.7 January
Parachipteria punctata	31.9 January	7.4 March	43.7 March	16.5 April
Steganacarus magnus	95.1 Septemb.	39.8 May	90.6 July	37.5 March
Steganacarus striculus	23.9 July	7.2 Novemb.	22.4 July	4.2 April
Oppia-Suctobelba sp.	7.0 April	2.9 August	8.2 March	2.6 Septemb.
Nanhermannia sp.	44.5 February	9.5 July	26.2 Septemb.	5.6 June
"other oribatids"	36.4 January	13.6 Novemb.	49.7 December	22.9 Septemb.
Total Oribatei	368.0 Septemb.	200.7 Novemb.	440.1 December	285.6 Septemb.

1969. This is readily explained by the changing age-structure composition of *P. peltifer*. The maximum density in August 1968 is due mainly to the influx of larvae into the population which contribute little to the population biomass; in contrast in April 1969 the population of this species is dominated by the much heavier adult stage.

The monthly biomass for the total oribatid population ranged from 200.7 to 368.0 mg dwt m^{-2} (mean 276.6) in the first year of the study and from 285.6 to 440.1 mg dwt m^{-2} (mean 338.4) in the second. PETERSEN (in preparation) summarises much of the known biomass data for oribatid mites from several habitats. In general the mean monthly biomass data from Meathop Wood for the total oribatid population falls within the range of values given by that author for temperate deciduous forest systems (41—1000 mg dwt).

5. Estimation of calorific values

5.1. Prefatory note

To express biomass in terms of energy units it is necessary to obtain a series of calorific equivalents. Little information exists in the literature for oribatid mites with the exception of WALLWORK (1973), NAESS, STEIGEN & SOLHØY (1975) and LUXTON (1975). LUXTON (1975) has pointed out that the energy content of animal material may vary for a number of reasons and that intensive measurements of energy flow through natural systems should probably take note of this. Unfortunately to obtain sufficient material for calorific studies it is often necessary to bulk material collected throughout the year. Consequently in this study no attempt was made to investigate the seasonal variations in the calorific value of oribatid mites.

5.2. Methods

Live material was extracted from soil and litter using a Tullgren funnel. The material was dried in a desiccator containing calcium chloride for seven days, pelleted and combusted in a micro-bomb

calorimeter similar to that described by PHILLIPSON (1964). Potential food material was also combusted. All the leaves used to obtain calorific values were collected at leaf-fall.

5.3. General remarks

The calorimeter data are given in Tables 6 and 7. The range of values obtained for oribatid mite material was 13.902 to 28.0512 kJ (3.3380 to 6.7001 Kcals) g dwt ash-free (mean 4.7916). This range is greater than that given by LUXTON (1975) of 14.444 to 21.980 kJ (3.450 to 5.250 Kcals) g dwt ash-free but if the single figure given in the present study for *Ceratoppia bipilis* (HERMANN) is ignored then the range of values are comparable. Generally the values obtained for individual species are similar to those previously published. The limited results for the immature stages seem to support the view of LUXTON (1975) that the values are approximately equivalent to those found for the adults.

The range of values obtained for higher plant material [17.9823 to 21.123 kJ (4.2950 to 5.1620 Kcals) g dwt ash-free] and for fungal material [17.4003 to 18.4261 kJ, (4.1560 to 4.4010 Kcals) g dwt ash-free] are less than that for the animal material. However the mean calorific value for higher plant material [19.7366 kJ (4.7140 Kcals) g dwt ash-free] is similar to that obtained for oribatid mite material. The mean value for fungal material [17.9132 kJ (4.2785 Kcals) g dwt ash-free] is noticeably less.

6. Respirometry

6.1. Prefatory note

Respiratory metabolism is a convenient parameter for assessing the significance of a population in the diffusion of energy through an ecosystem. Respiratory data for oribatid mites has been collected by ENGELMANN (1961), ZINKLER (1966), BERTHET (1964), WEBB (1969, 1975), WEBB & ELMES (1972), WOOD & LAWTON (1973), LUXTON (1975) and BLOCK (1977). Most of these data refer to adult respiration, although estimates for the immature stages of *Parachipteria willmanni*, *Damaeus onustus* C. L. KOCH and *Nothrus palustris* C. L. KOCH [WOOD & LAWTON 1973], *N. silvestris* [WEBB 1969], *S. magnus* [WEBB 1975] and *Alaskozetes antarcticus* (MICHAEL) [BLOCK 1977] have been made. Several studies have highlighted the influence of temperature on oribatid mite respiration (BERTHET 1964; WEBB 1969; LUXTON 1975 and BLOCK 1977).

Table 6. Calorimetry of oribatid mites

Species	kJ g dwt ash-free (± S. E.)	kJ g dwt	% ash	Replicates
Nothrus silvestris	20.976 ± 1.424	19.577	6.67	3
Nothrus silvestris (juveniles)	21.265	19.628	7.70	1
Platynothrus peltifer	18.635 ± 0.963	17.726	4.88	5
Hermannia gibba	19.608 ± 0.368	17.920	8.61	7
Hermannia gibba (juveniles)	17.920	16.486	8.00	1
Parachipteria punctata	22.420	19.326	13.80	1
Steganacarus magnus	13.976 ± 0.666	8.627	38.27	8
Hermanniella granulata	17.702 ± 0.871	15.914	10.10	5
Ceratoppia bipilis	28.052	25.468	9.21	2

Table 7. Calorimetry of potential food (litter) types

Species	kJ g dwt ash-free (± S. E.)	kJ g dwt	% ash	Replicates
Quercus sp.	21.612	20.705	4.20	1
Fraxinus excelsior	19.180 ± 0.419	18.547	3.30	4
Corylus avellana	17.982 ± 0.121	17.452	2.95	4
Fagus sylvatica LINNAEUS	19.356 ± 0.297	19.055	1.55	4
Betula sp.	20.553 ± 0.381	19.920	3.08	4
Mycena galopus (FRIES) KUMMER				
Grown on hazel	18.426 ± 0.100	18.048	2.05	4
Grown on oak	17.400 ± 0.172	16.908	2.83	3

6.2. Methods

Animals were extracted from fresh soil and litter using a Tullgren funnel. Individuals of three species (*N. silvestris*, *P. peltifer* and *H. gibba*) were identified and placed in culture jars at the temperature at which respiratory activity was to be measured (15 °C). The respiratory rates of the mites were measured in a Cartesian Diver respirometer (Holter 1943, Linderstrøm-Lang 1943) using stoppered divers (Zeuthen 1964). Measurements were usually conducted on single animals. However, for certain immature stages, up to three individuals of the same species and life-stage, were placed together and a mean value for oxygen consumption obtained. The live weight of each animal was determined, and the life-stage confirmed at the termination of each experiment.

6.3. General remarks

The respiratory data are given in Table 8. The results for the immature and adult stages of *N. silvestris* can be compared to those obtained for adults by Berthet (1964) and for

Table 8. Respiratory rates for three species of oribatid mites at 15 °C

Species	Life stage	$\mu l\ O_2 \times 10^{-3} ind^{-1} hr^{-1} \pm SD$	$\mu l\ O_2\ g\ lwt\ hr^{-1}$	n
Nothrus silvestris	Adult	16.54 ± 4.01	292.7	9
	Tritonymph	13.00 ± 3.52	382.3	13
	Deutonymph	9.25 ± 2.95	608.6	10
	Protonymph	5.38 ± 2.36	707.9	10
Platynothrus peltifer	Adult	18.83 ± 8.00	315.0	9
	Tritonymph	15.75 ± 0.54	423.4	3
	Deutonymph	7.92 ± 2.94	546.2	6
Hermannia gibba	Adult female	40.04 ± 8.25	193.4	14
	Adult male	31.50 ± 8.88	183.1	8
	Tritonymph	23.92 ± 8.97	238.0	14
	Deutonymph	17.50 ± 6.84	397.7	5
	Protonymph	12.25 ± 7.31	696.0	6

equivalent life-stages by Webb (1969). The results given by Webb were corrected, where necessary, to 15 °C using the empirical relationship between oxygen consumption and temperature derived by that author. The adult value (292.7 $\mu l\ O_2\ g\ lwt\ hr^{-1}$) is higher than that obtained for adults by Berthet (214.7 $\mu l\ O_2\ g\ lwt\ hr^{-1}$) and for non-breeding adults by Webb (137.5 $\mu l\ O_2\ g\ lwt\ hr^{-1}$), but comparable to that found for gravid adults by Webb (304.7 $\mu l\ O_2\ g\ lwt\ hr^{-1}$). Comparison of the weight specific oxygen consumption rates of immatures reveals that for each juvenile stage considered the values are higher than those given by Webb. This trend continues when the value for adult *P. peltifer* (315 $\mu l\ O_2\ g\ lwt\ hr^{-1}$) is compared to that given by Berthet (164.5 $\mu l\ O_2\ g\ lwt\ hr^{-1}$). Wood & Lawton (1973) also recorded differences of this magnitude for certain species, particularly *P. willmanni* and *Euzetes globulus* (Nicolet), and suggests that they may represent real differences between different populations or that they may be due to errors inherent in the technique and apparatus peculiar to each laboratory. No comparable data for the juveniles of *P. peltifer* or for any life-stage of *H. gibba* are known.

It is clear from Table 8 that the youngest stages measured have the highest weight specific respiratory rates and that all the immatures have higher rates than the adults. This has also been found by Wood & Lawton (1973) for *P. willmanni*, *D. onustus* and *N. palustris*. Certain deviations from this overall trend have been found for *N. silvestris* [Webb 1969], *S. magnus* (Webb 1975) and *A. antarcticus* [Block 1977]. Indeed Webb showed that gravid adults possessed a higher rate than all stages except the protonymph and suggested that this elevated was associated with egg production. Contradictory findings were given by Wood & Lawton (1973) for *P. willmanni* and *D. onustus* where gravid females had the lowest rate of all life-stages investigated. Comparison of the weight specific oxygen uptake within the immature stages shows little consistent pattern. Only for *D. onustus* [Wood & Lawton 1973] does the rate progressively decline from the larval to the tritonymphal

stage. In other species the highest rate was shown by the protonymph of *N. silvestris* [WEBB 1969], the larva of *N. palustris* [WOOD & LAWTON 1973], and the deutonymphs of *P. willmanni* [WOOD & LAWTON 1973], *S. magnus* [WEBB 1975] and *A. antarcticus* [BLOCK 1977]. WEBB (1975) suggests that instars which deviate from the overall trend may be those that are subject to important changes in their habitat or life-cycle and if, for example, this took the form of dispersal then they would presumably be both physically and metabolically more active than others. The converse of this could be that of a life-stage is more capable of surviving adverse environmental periods by reducing its metabolic rate. Another possible explanation involves the nutritional biology of the immature stages. LUXTON (1972) claims evidence that different fungal food material was being selected for by each of the developmental stages of *Hermannia pulchella* WILLMANN. In addition HARTENSTEIN (1962a) has shown that *Belba kingi* HARTENSTEIN juveniles develop more rapidly when confined to a diet of *Trichoderma* sp. If, therefore, the availability of preferred foods influences the developmental rate, then it is probable that this will be reflected in their metabolic rate. However, insufficient information on several aspects of immature stage biology prevents any firm conclusions from being drawn.

7. Population metabolism

7.1. Prefatory note

One of the major factors faced when laboratory-based respiratory data is extrapolated to field populations is the influence of temperature upon respiratory rate in poikilothermic animals. When information is limited i. e. restricted to a few species and a single temperature, it is normal to derive a relationship between body weignt and oxygen consumption and use this to predict respiration rates for those animals not directly measured. A standard metabolic/temperature curve (e. g. KROGH 1914) is then often used to estimate respiration rates for a range of temperatures comparable to those experienced by the organisms in the field. Recently however, multiple regression equations correlating respiration rates, body weight and temperature have been derived for nine species of adult oribatids (LÖXTON 1975) and for an antarctic oribatid *A. antarcticus* [BLOCK 1977]. In addition LUXTON has shown that, in the main, feeding associations appear to be closely related to the pattern of oxygen uptake at various temperatures with the macrophytophages being lowest, the panphytophages highest and the microphytophages occupying an intermediate level. It is apparent therefore that the combination of limited data with a standard metabolic curve will produce a less accurate estimate of population metabolism than is otherwise possible. Consequently it was decided that the respiratory rates for individual species and species-groups would be predicted from the appropriate multiple regression equations given by LUXTON (1975). It is considered that the estimate of population metabolism, using this procedure, will be more meaningful for the following reasons; the data from which the equations are derived are more comprehensive than those of the present study; the equations permit the oribatid population at Meathop Wood to be divided into their major feeding groups; the effect of temperature upon respiration rate is allowed for; the predicted respiration rates for all life-stages of the panphytophages *N. silvestris*, *P. peltifer* and *H. gibba* compare more favourably with the direct measurements of the present investigation than with those currently available in the literature; the prediction of respiratory rates from body weight — oxygen consumption relationships can be misleading when applied to a species of markedly different body form. This last point is well illustrated by a consideration of adult *S. magnus*. Several authors have measured the oxygen consumption of adult *S. magnus* directly (BERTHET 1964, 82.4 μl O_2 g lwt hr^{-1} at 14 °C; WEBB & ELMES 1972, 69.0—144.3 μl O_2 g lwt hr^{-1} at 18 °C; LUXTON 1975, 111.0 μl O_2 g lwt hr^{-1} at 15 °C and WEBB 1975, 69.8—128.2 μl O_2 g lwt hr^{-1} at 18 °C). No direct measurements of the oxygen consumption of this species were made in this study. In order to predict the respiration rate of *S. magnus* an equation relating the log of oxygen consumed (R) at 15 °C (μl $O_2 \times 10^{-3}$ ind^{-1} hr^{-1}) and the log of body live weight (W, μg) was derived from the data (Table 8) collected in this investigation for all the life-stages of *N. silvestris*, *P. peltifer* and *H. gibba*. The equation $\log R = 0.2380 + 0.5885 \log W$ describes this relationship and the respiratory rate of an adult *S. magnus* (of live weight 270.4 μg) predicted from this is 172.6 μl O_2 g lwt hr^{-1} at 15 °C. This value is appreciably higher than the direct measurements quoted earlier. This difference is not unexpected as the equation is derived from data for species whose bodies contain much smaller proportions of inert material than that of *S. magnus* and therefore a respiratory estimate for this species based solely on body weight will be inflated.

7.2. Methods

The multiple regression equations (LUXTON 1975) for *Steganacarus magnus*, *Steganacarus spinosus* (SELINICK) and *Achipteria coleoptrata* were used to estimate the respiration rates of *S. magnus*,

S. striculus and *P. punctata* respectively. This is valid as *S. spinosus* is similar in both body form and dry weight to *S. striculus*, as is *A. coleoptrata* to *P. punctata*. *N. silvestris*, *P. peltifer*, *H. gibba* and *Nanhermannia* sp. are collectively regarded as panphytophages, and *T. velatus* and the species-group *Oppia-Suctobelba* as microphytophages (LUXTON 1972). The appropriate regression equation was used in each case. The respiration rate of each juvenile stage of the five species for which age-structure data were available was also predicted by application of the relevant regression equation. The regression equation given for total oribatids (including macrophytophages) was used for estimating the respiration rates for the species-group "other oribatids".

The respiratory rates, corrected for mean monthly soil temperatures, were computed with population density and age-structures data to provide estimate of population metabolism. Oxygen consumption was converted to energy units using the calorific equivalent of SLOBODKIN (1962) of 20.1 J (4.8 cals) per ml O_2 (assuming an RQ of 0.82).

7.3. General remarks

The population metabolism of each species and species-group for each year of the investigation is given in Table 9. The major contributor to total oribatid metabolism in both years was *H. gibba*, 22.0 and 26.0 % respectively. In contrast *T. velatus* contributed only

Table 9. Estimates of oribatid population metabolism (kJ $m^{-2}yr^{-1}$) in each year of the study

Species or species group	Year 1	Year 2
Nothrus silvestris	1.980	2.202
Platynothrus peltifer	1.131	1.696
Hermannia gibba	2.902	4.463
Tectocepheus velatus	0.293	0.373
Parachipteria punctata	1.030	1.855
Steganacarus magnus	0.821	0.812
Steganacarus striculus	0.498	0.528
Oppia-Suctobelba sp.	0.632	0.586
Nanhermannia sp.	1.712	1.256
„other oribatids"	2.206	3.148
Total Oribatei	**13.205**	**16.919**

2.2 % in each year. The total population metabolism increased from 13.2051 kJ (3.154 Kcals) $m^{-2}yr^{-1}$ in year 1 to 16.919 kJ (4.041 Kcals) m^{-2} yr^{-1} in year 2, a difference of 28.1 % between years. This increase cannot be attributed to any one particular component of the population as most groups had a higher value for population metabolism in year 2. The greatest increases were shown in *P. punctata* (80.0 %) and *H. gibba* (54.0 %), and the largest decrease by *Nanhermannia* sp. (26.7 %).

BERTHET (1964) suggested that the contribution of juveniles to total population metabolism could be two to three times that of the adult. WEBB (1970) recorded that 51.5 % of the population metabolism of *N. silvestris* could be attributed to the immature stages. Comparable values were found for the immatures of *N. silvestris* in this study (67.0 and 65.0 % in year 1 and 2 respectively). However the contribution of juvenile *P. peltifer*, *H. gibba*, *P. punctata* and *T. velatus* was lower, ranging from 24.3 % (*T. velatus*) to 40.2 % (*P. peltifer*) in year 1, and from 31.6 % (*P. punctata*) to 39.5 % (*H. gibba*) in year 2. The higher juvenile contribution of *N. silvestris* can be attributed to the greater occurrence of these life-stages in the population (82.2—85.9 %) when compared to that of the other four species (54.6 to 67.6 %). The evidence from the present study therefore indicates that the immature contribution to total population metabolism is approximately 70 % that of the adult although this proportion may vary according to the age-structure composition.

The energy dissipated in respiratory metabolism by field populations of oribatid mites is low in temperate deciduous woodlands, ranging from 8.4 to 46.9 kJ (2.0 to 11.2 Kcals) m^{-2} yr^{-1} (MACFADYEN 1963). Similar values have been obtained by VAN DER DRIFT (1974) for oribatids of a *Quercus* woodland [41.868 kJ (10 Kcals) m^{-2} yr^{-1}] and by KITAZAWA (1971) for "Acari" of a temperate deciduous woodland [7.74 kJ (1.85 Kcals) m^{-2} yr^{-1}]. The

values from this study [13.205—16.919 kJ (3.154—4.041 Kcals) m^{-2} yr^{-1}]. are within the range given by these authors.

Little information exists regarding the population metabolism of individual oribatid species. WEBB (1970) gives 2.378 kJ (0.568 Kcals) m^{-2} yr^{-1} for a population of *N. silvestris* and MITCHELL (1975) 0.736 kJ (0.176 Kcals) m^{-2} yr^{-1} for a *Ceratozetes* sp. population. The figures for *N. silvestris* from the present study [1.980—3.102 kJ (0.473—0.526 Kcals) m^{-2} yr^{-1}] are comparable to that obtained by WEBB. This similarity is somewhat surprising when the differences in mean monthly biomass between the two populations is considered, 71.55 mg dwt m^{-2} (WEBB) compared to 25.8—31.6 mg dwt m^{-2} (present study). [The figure 71.55 was calculated using the data of WEBB (1969, 1970) and using a dry to wet weight relationship of 0.45]. However, a closer analysis reveals that in WEBB's study the highest biomass peak occurred between January and April when field temperatures were low, followed by a secondary biomass peak in November when the field temperatures were declining from the July high. In contrast at Meathop Wood peaks of biomass occurred in August when the field temperatures were high, with a further peak in April/May when the field temperatures were rising. Thus the timing of biomass peaks and the established influence of temperature upon respiration rate could well account for the similar population metabolism estimates, despite the substantial differences in mean population biomass.

8. Estimation of rejecta

8.1. Prefatory note

The influence of temperature and food type upon the rate of faecal pellet deposition was investigated in the laboratory. Leaves of oak, ash and hazel were chosen as food items. There species of oribatid mites, *N. silvestris*, *P. peltifer* and *H. gibba* were chosen for the feeding experiments. All the oribatid species selected have been described as panphytophages (LUXTON 1972) and collectively represent almost 50% of the total mean monthly biomass of Oribatei at Meathop Wood.

8.2. Methods

The leaves of oak, ash and hazel were collected at leaf-fall and subjected to the following treatment in the laboratory; immersion in water for the first two weeks; enclosure in muslin bags, 5.5 meshes to the cm, within fresh soil and litter for a further two weeks; finally immersion in water for two weeks. Leaf squares, 1×1 cm, were then cut and brushed to remove any loose surface material before being offered as food. The feeding experiments were conducted in 3.8×1.9 cm glass vials containing a plaster of Paris medium. A small circle of filter paper was placed in the lid of the vial and secured by gauze. The lid was perforated to permit air flow. The filter paper and substrate were kept damp to maintain a high humidity but any residual water was removed. Four to eight animals of the same species and developmental stage were placed in each culture vial and offered one food type at a time. Feeding experiments were conducted at temperatures within the range 4 to 26 °C. Faecal pellets were removed daily from the cultures for a period of seven days.

8.3. General remarks

The rates of faecal pellet deposition at the temperatures investigated and the food types offered are given in Table 10, and illustrated in Figs. 9—14.

The regression equations of log number of faecal pellets produced per individual per day (D. R.) on all readily accepted food materials) against temperature (T °C) were calculated:

N. silvestris adults	log D. R. = 0.0573 T — 0.3701
N. silvestris immature	log D. R. = 0.0532 T — 0.3701
N. silvestris all stages	log D. R. = 0.0550 T — 0.3679
P. peltifer adults	log D. R. = 0.0614 T — 0.2166
H. gibba adults	log D. R. = 0.0566 T — 0.4749
Overall all stages equation	log D. R. = 0.0566 T — 0.3539

The results at 26 °C were not included in the regression calculations as this temperature is far in excess of the highest soil temperature at Meathop Wood.

The adults of *N. silvestris* accepted oak, ash and hazel as a food source. The number of faecal pellets produced by an adult *N. silvestris* per day was higher when fed upon hazel

Table 10. Mean number of faecal pellets produced per individual per day (± S. E.) when offered oak, ash and hazel at various temperatures

Stage	Food type	4 °C	8 °C	10 °C	15 °C	20 °C	26 °C
Nothrus silvestris							
Adult	Oak	0.50	—	1.56 ±0.06	3.00 ±0.21	5.66 ± 0.22	—
	Ash	0.44	1.80 ±0.22	—	2.43 ±0.12	—	7.83 ±0.84
	Hazel	—	—	2.43 ±0.51	3.80 ±0.12	7.91 ± 0.61	6.17 ±0.23
Tritonymph	Oak	—	—	1.33 ±0.26	2.60 ±0.19	5.05 ± 0.56	—
	Ash	—	1.80 ±0.20	—	2.40 ±0.06	—	6.20 ±0.54
Deutonymph	Oak	—	—	1.36 ±0.13	—	5.21 ± 0.16	—
Platynothrus peltifer							
Adult	Oak	—	—	2.73 ±0.13	—	8.70 ± 0.85	—
	Ash	0.95 ±0.08	2.14 ±0.13	—	4.43 ±0.66	12.90 ± 0.90	9.93 ±0.52
Hermannia gibba							
Adult	Ash	0.50 ±0.02	1.25 ±0.29	—	2.20 ±0.22	5.20 ± 0.72	7.04 ±0.74

*) Litter only.

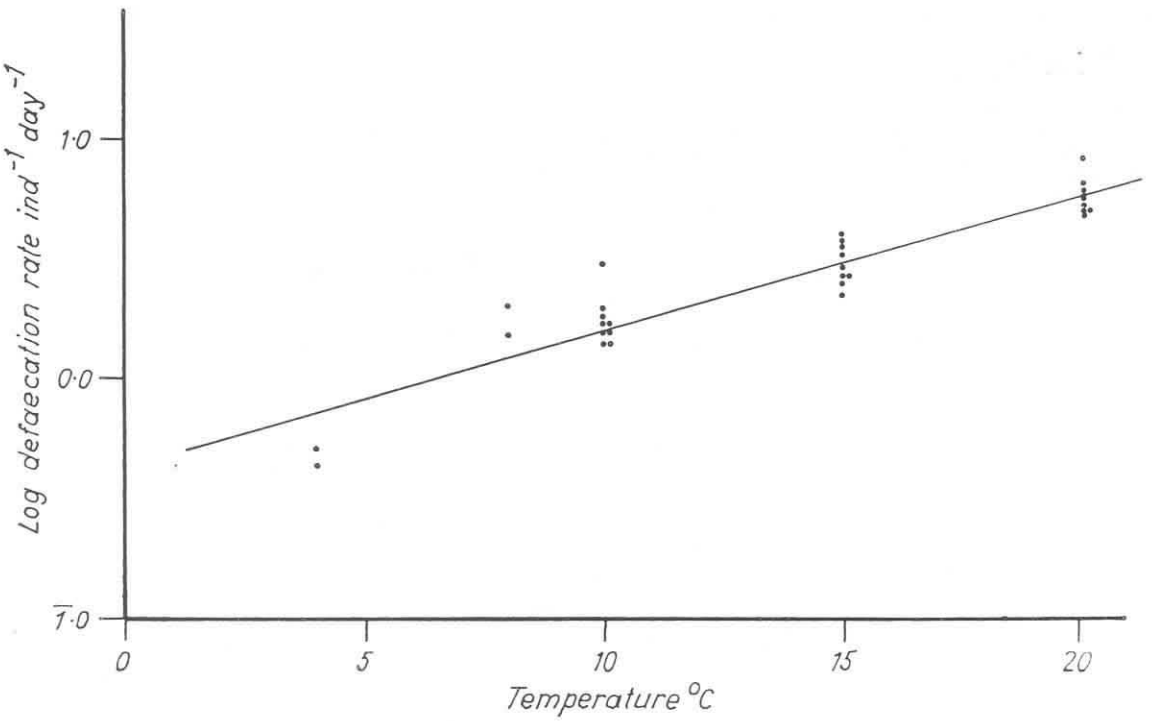

Fig. 9. The relationship between log defaecation rate and temperature (°C) for *Nothrus silvestris* adults when offered oak, ash and hazel as a food source (each symbol (·) denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

than when fed on oak and ash at equivalent temperatures within the range 4—20 °C. There were no significant differences between the adult and immature defaecation rates of this species when offered identical food material.

The adults of *P. peltifer* readily accepted oak and ash but feeding on hazel only occurred at 26 °C and then at a low rate with the production of only 1.95 faecal pellets per individual per day. The defaecation rate of this species when fed on oak and ash was higher than that

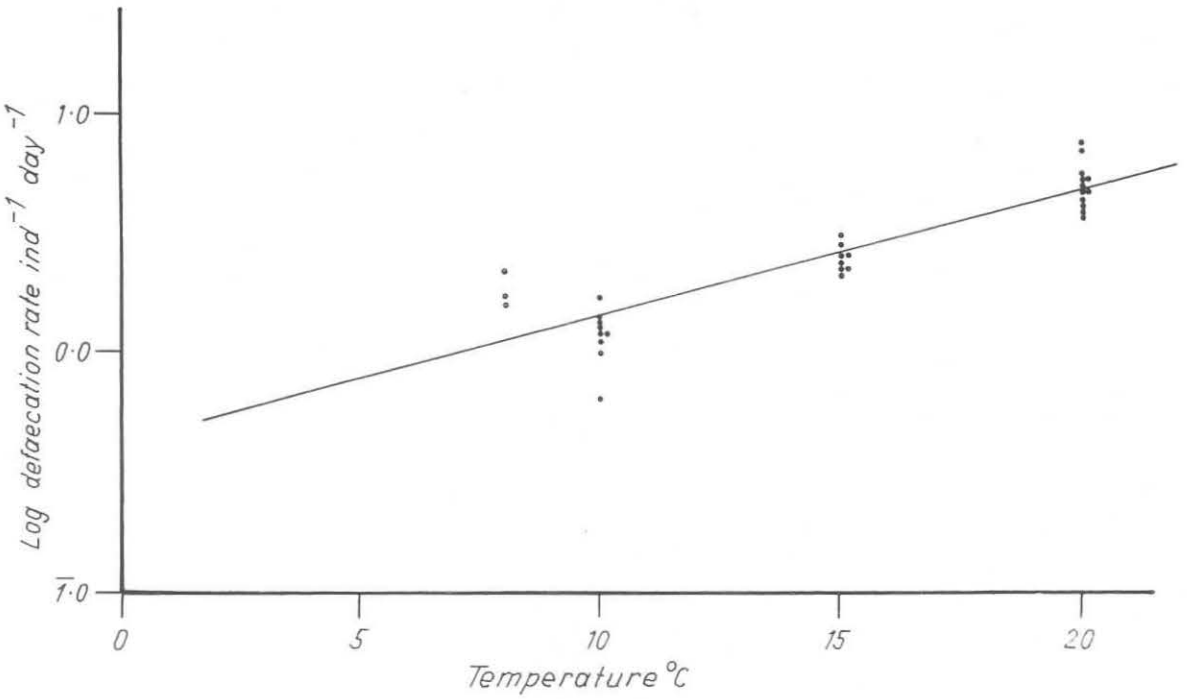

Fig. 10. The relationship between log defaecation rate and temperature (°C) for *Nothrus silvestris* juveniles when offered oak and ash as a food source (each symbol [·] denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

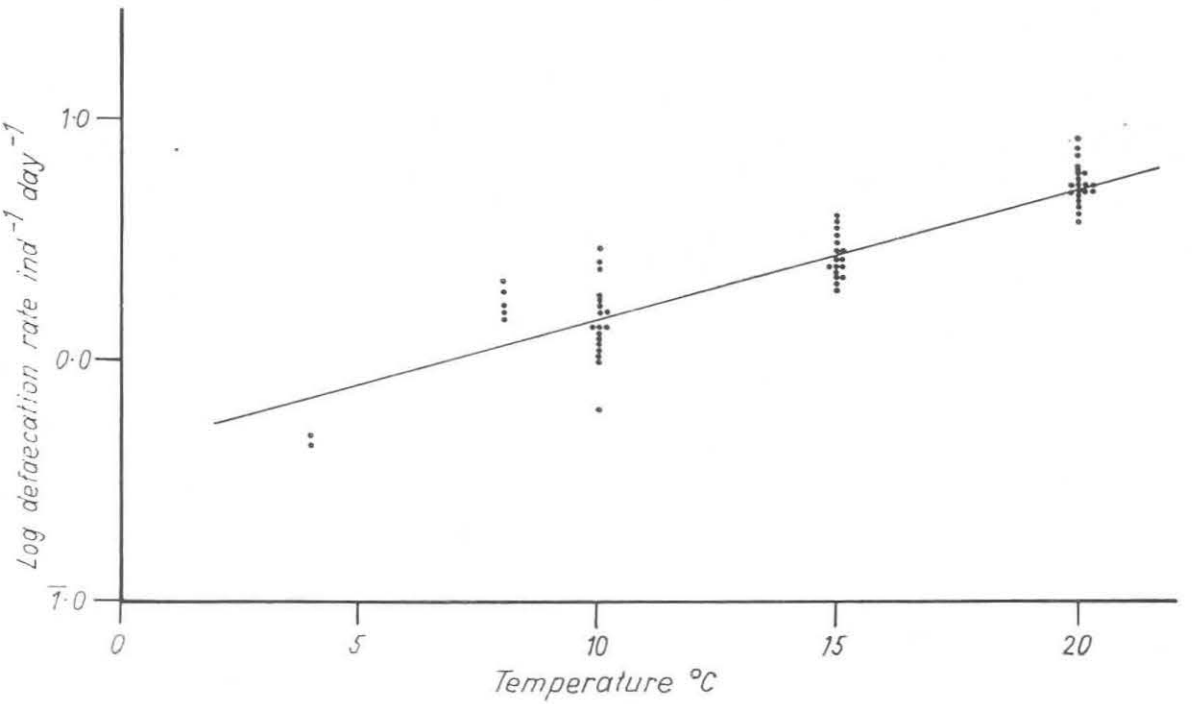

Fig. 11. The relationship between log defaecation rate and temperature (°C) for the adult and juvenile stages of *Nothrus silvestris* (each symbol [·] denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

for the other oribatid species studied at all of the temperatures investigated. HARTENSTEIN (1926b) recorded the feeding rate of *P. peltifer* at 20 °C and observed that it fed voraciously, producing more than 30 faecal pellets per individual per week, when offered the fungi *Stemphylium* sp. and *Phialophera mustea* NURGAARD. He also observed that *P. peltifer* was capable of producing an average of 8 pellets per day when fed on sugar maple leaves decayed aseptically with *Lenzites trabea* (PERSOON). This figure is similar to that recorded in the present study when the adults of this species were offered oak at 20 °C, but noticeably less than that when fed on ash at the same temperature.

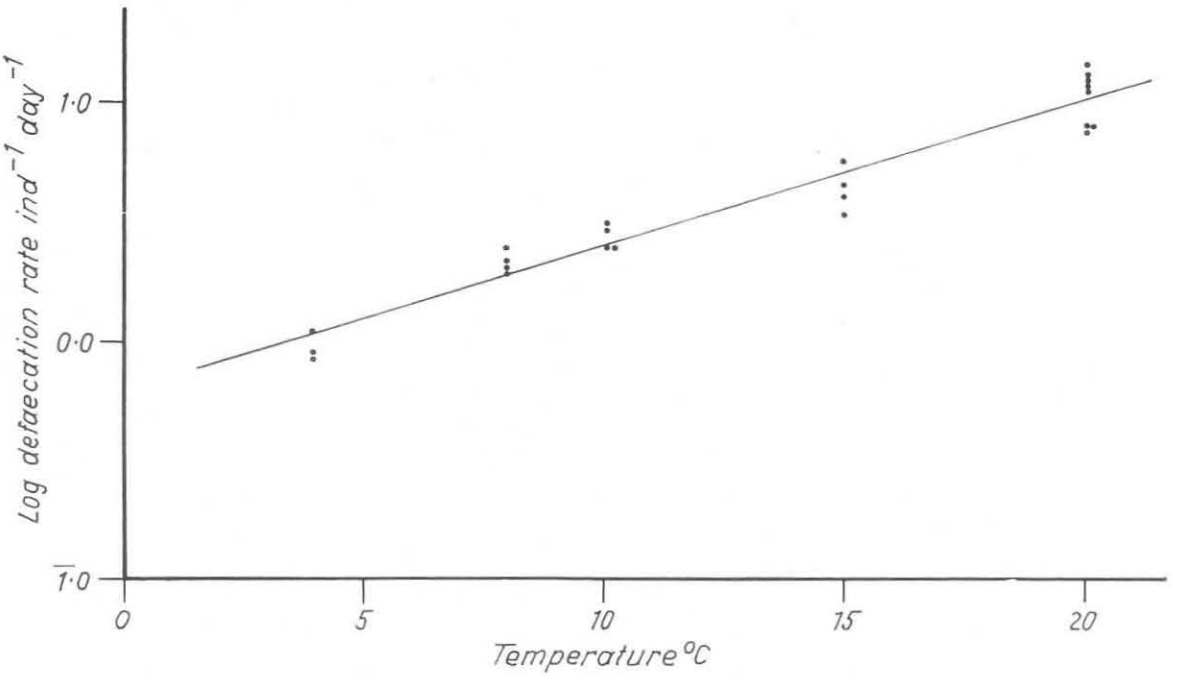

Fig. 12. The relationship between log defaecation rate and temperature (°C) for *Platynothrus peltifer* adults when offered oak and ash as a food source (each symbol [·] denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

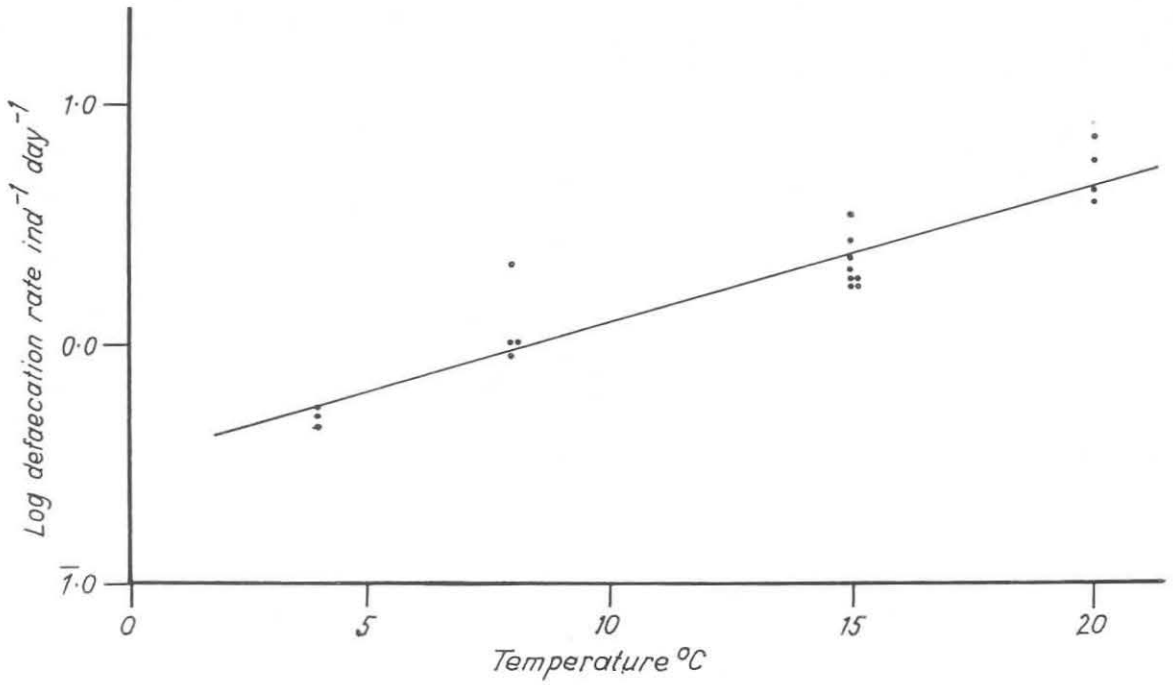

Fig. 13. The relationship between log defaecation rate and temperature (°C) for *Hermannia gibba* adults when offered ash as a food source (each symbol [·] denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

The adults of *H. gibba* readily accepted ash but feeding on oak was very restricted and no faecal material was observed when this species was offered hazel. HARTENSTEIN (1962b) observed that more than 30 faecal pellets were produced per individual per week when this species was offered decaying leaves and wood as compared to less than 5 pellets when fed on *Cladosporium cladosporioides* (FRESENIUS) DE VRIES and *Hormodendrum cladosporioides* (FRESENIUS) SACCARDO at 20 °C.

All of the three species investigated showed an exponential rise in defaecation rate on readily accepted food materials within the temperature range, 4 to 20 °C. No significant rise in defaecation rate was observed between 20 and 26 °C. The three oribatid species studied

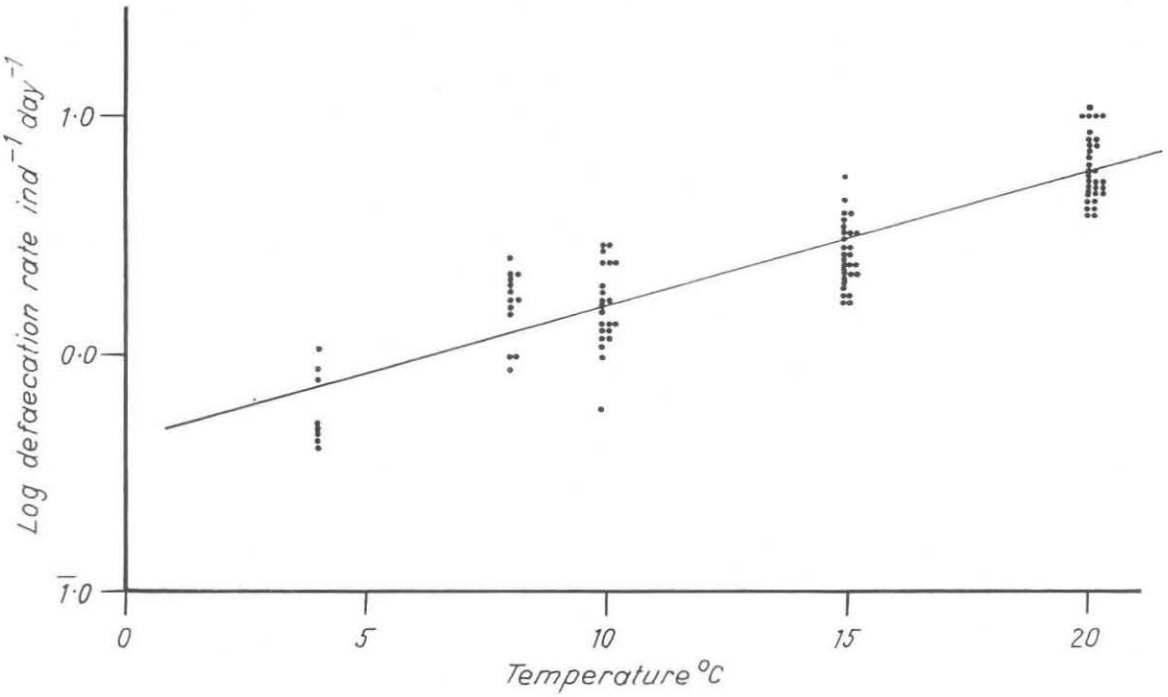

Fig. 14. Composite data showing the relationship between log defaecation rate and temperature (°C) for *Nothrus silvestris*, *Platynothrus peltifer* and *Hermannia gibba* (each symbol [·] denotes the mean number of faecal pellets ind^{-1} day^{-1} produced by one culture at a particular temperature).

have been described as nonspecialised feeders or panphytophages (SCHUSTER 1956, LUXTON 1972). The evidence from these, albeit limited, experiments indicate that even within this broad feeding group some selectivity occurs. However as HARTENSTEIN (1962b) points out the condition of field food materials cannot be duplicated in the laboratory and consequently the results of feeding experiments must be viewed with caution.

8.4. Faecal biomass

Adults of *N. silvestris*, *P. peltifer* and *H. gibba* were fed on ash at 20 °C. The faecal pellets produced by each species within the first 24 hours were removed, dried and weighed in batches of sixty. A mean faecal pellet dry weight was obtained for each species and expressed as a percentage of adult dry weight (Table 11). Assuming that faecal pellet dry weight is

Table 11. The dry weight (μg $\pm$ S. E.) of adult faecal pellets expressed as a percentage of adult dry weight

Species	Mean dry weight of faecal pellet	% faecal pellet dry weight adult dry weight
Nothrus silvestris	0.59 $\pm$ 0.08	2.24
Platynothrus peltifer	0.45 $\pm$ 0.01	1.65
Hermannia gibba	1.53 $\pm$ 0.23	1.94
Mean		**1.94**

a constant function of body dry weight and equating this with the appropriate equation relating defaecation rate and temperature, mean monthly soil temperatures, population density and age-structure data, the total amount of faecal biomass produced in each year of the study by *N. silvestris*, *P. peltifer* and *H. gibba* was calculated (Table 12). The faecal biomass of the other species and species-groups was calculated in a similar manner by utilising the overall equation relating defaecation rate and temperature. The calorific value of faecal material was not estimated in this investigation. Consequently faecal biomass was converted to energy units using the mean calorific equivalent for potential foods, 18.662 kJ (4.4574 Kcals) g dwt, obtained from the calorimetry studies. The energy content of the faecal mate-

Table 12. The faecal biomass (mg dwt m^{-2}) produced in each year of the investigation by the oribatid population

Species or species-group	Year 1	Year 2
Nothrus silvestris	348.37	390.29
Platynothrus peltifer	257.69	403.69
Hermannia gibba	615.87	953.27
Tectocepheus velatus	22.25	30.16
Parachipteria punctata	163.68	294.28
Steganacarus magnus	700.64	686.64
Steganacarus striculus	129.22	142.09
Oppia-Suctobelba spp.	43.99	41.53
Nanhermannia spp.	201.16	149.97
"other oribatids"	258.15	375.01
Total Oribatei	2741.02	3466.93

rial rejected by the total oribatid population was thus estimated as 51.154 kJ (12.218 Kcals) m^{-2} in year 1 and 64.389 kJ (15.453 Kcals) m^{-2} in year 2 of the investigation.

9. Estimation of assimilation and consumption

9.1. Methods

A gravimetric method was used for the estimation of adult assimilation rates. A number of discs were cut from oak and ash leaves which had been treated in a similar manner to those used for the estimation of defaecation rates. Before being weighed the leaf discs were dried for seven days in a desiccator containing calcium chloride. They were then soaked in water for three days before being offered as food.

Five cultures of adult *P. peltifer* and *H. gibba* were offered ash leaves, three cultures of adult *N. silvestris* were offered ash and four offered oak as a food source. The faecal pellets produced by each culture were removed daily and stored on filter paper pans in a desiccator. When the leaf discs showed signs of fragmentation they were removed and also stored in a desiccator prior to weighing. The assimilation efficiency of each species was then calculated from the following equation after taking into account control culture losses:

$$\text{Assimilation efficiency} = \frac{\text{dry weight of food ingested} - \text{dry weight of reject}}{\text{dry weight of food ingested}} \times \frac{100}{1}$$

9.2. General remarks

The assimilation efficiencies of adult *N. silvestris* ranged from 15.9 to 47.2 % (mean 34.8 %) when fed on oak, and from 56.5 to 67.4 % (mean 61.8 %) when fed on ash. The overall assimilation effeciency of this species was 48.3 %. The range of assimilation efficienc ies of *P. peltifer* was 33.9 to 59.6 % (mean 46.3 %) and of *H. gibba*, 19.0 to 61.1 % (mean 42.9 %).

The assimilation efficiencies of oribatid mites have been investigated by MURPHY (1953), ENGELMANN (1961), BERTHET (1964), LUXTON (1972), WEBB & ELMES (1972) and STEIGEN, SOLHØY & GYLLENBERG (1975). The published data for adult *S. magnus*, considered to be a macrophytophage (LUXTON 1972), ranges from 12.0 % for adults (BERTHET 1964) to 58.3 % for newly moulted males (WEBB & ELMES 1972). LUXTON (1972) records values ranging from 46.7 to 65.7 % for the microphytophage, *Damaeus clavipes* (HERMANN). The estimates obtained in the present study for three panphytophages are intermediate in nature; the paucity of published data on assimilation efficiencies does not permit a direct comparison to be made. LUXTON (1972) suggested that assimilation efficiencies may be related to feeding preferences. However the highly variable results of *S. magnus*, the only species studied by several authors, indicates that any further consideration of this suggestion at this point would be imprudent. Nevertheless, evidence is accumulating that the assimilation efficiencies of oribatid mites are higher than previously considered.

The daily consumption rates of adult *N. silvestris*, *P. peltifer* and *H. gibba* (at temperatures comparable to those experienced by these organisms in the field, 5, 10 and 15 °C),

Table 13. The consumption and assimilation rates of oribatid mites

Species	Temperature °C	Consumption of % body dwt day	% $\frac{A}{C}$	Author
Steganacarus magnus adults	5	1.5	50.0	MURPHY (1953)
Steganacarus magnus adults	18	2.0	12.0	BERTHET (1964)
Steganacarus magnus				
Mature ♂♂	18	5.7	19.1	WEBB and ELMES (1972)
Newly moulted ♂♂	18	8.1	58.3	
Mature ♀♀	18	2.8	52.9	
Newly moulted ♀♀	18	7.6	58.1	
Oribatulidae	20	1.7	—	MCBRAYER and REICHLE (1971)
Camasiidae	20	2.3	—	
Carabodidae	20	2.5	—	
Cymbaeremaeidae	20	9.0	—	
Oribatei IX	20	5.4	—	
Phthiracaridae	20	1.0	—	
Carabodes labyrinthicus Adults	10	1.4	41.0	STEIGEN et al. (1975)
Damaeus clavipes				
Adèlt	15	9.0	61.5	LUXTON (1972)
Tritonymph	15	5.5	46.7	
Deutonymph	15	7.0	65.7	
Protonymph	15	9.0	63.3	
Cultoribula juncta	20	25.0	—	KOWAL (1969)
Several species	25	40.0	20.0	ENGELMANN (1961)
Mature oribatids	6	1.4	—	KOWAL and CROSSLEY (1971)
	15	4.6	—	
	25	13.3	—	
	field	12.5	—	
Immature oribatids	6	2.6	—	
	15	2.0	—	
	25	7.6	—	
	field	5.9	—	
Nothrus silvestris				
Adults	5	3.6	—	
	10	6.9	—	
	15	13.4	—	
	20	—	48.3	
Platynothrus peltifer				Present study
Adults	5	3.8	—	
	10	7.7	—	
	15	15.6	—	
	20	—	46.3	
Hermannia gibba				
Adults	5	2.2	—	
	10	4.2	—	
	15	8.0	—	
	20	—	42.9	

were estimated by combining the relevant regression equations relating defaecation rate and temperature with the mean assimilation efficiencies calculated for each species. These values were then expressed as a percentage of adult dry weight and are given in Table 13. Data from other authors are included for comparative purposes. The estimates of consumption for all species ranged from 2.2 % of body dry weight per day for *H. gibba* at 5 °C to 15.6 % at 15 °C for *P. peltifer*. All species showed a rise in consumption rate with increasing temperatures similar to that described by KOWAL & CROSSLEY (1971). The calculated consumption rates are somewhat higher than most of the published data, especially after taking into account the influence of temperature. However they are appreciably lower than the 25.0 % given for *Cultoribula juncta* (MICHAEL) [KOWAL 1969] and 40.0 % for an undetermined species (ENGELMANN 1961). The value given by KOWAL & CROSSLEY (1971), 12.5 % for mature oribatids at field temperatures, suggests that the figures from the present study are not grossly inflated. This conclusion is supported to some extent by LUXTON (1972)

who comments that there is growing evidence to suggest that the panphytophagous mites process perhaps twice as much material as the macrophytophages.

The feasability of using assimilation and defaecation data obtained from the three panphytophages studied in order to estimate the consumption rates of the other species and species-groups not directly measured, was investigated by considering the case of adult *S. magnus*. This is the only species for which relatively comprehensive consumption data are available in the literature. By combining the overall regression equation relating defaecation rate and temperature together with the calculation of mean faecal pellet weight (1.94 % of body dry weight, Table 11) it was estimated that an adult *S. magnus* weighing 132.6 μg dwt (biomass data, Table 2) would defaecate 3.14 μg dwt per day at 7.8 °C (the mean monthly soil temperature at Meathop Wood). This figure in combination with the mean assimilation efficiencies obtained for *N. silvestris*, *P. peltifer* and *H. gibba* represents a consumption rate of 4.37 % of body dry weight per day by adult *S. magnus*. This figure is within the range 1.5 to 8.1 %, given by MURPHY (1953), BERTHET (1964) and WEBB & ELMES (1972) for adults of this species. This comparison is perhaps invalid as most consumption studies on *S. magnus* have been undertaken at 18 °C and it has been shown that temperature affects defaecation rate and presumably consumption rate. Nevertheless the lack of sufficient published data seems to justify the extrapolation between species and species-groups for which defaecation and assimilation data were not available. Consequently the total consumption by the oribatid mite population was calculated as 5.06 g dwt m^{-2} in year 1 and 6.40 g dwt m^{-2} in the second year of the investigation. These values were converted to energy units using the mean calorific equivalent for potential foods 18.6622 kJ (4.4574 Kcals) g dwt, obtained from the calorimetry studies.

10. Net production

10.1. Prefatory note

The concept of net production is one which has any aspects and interpretations. Definitions of net production are often idealised and can only be applied to relatively few "suitable" populations. Nevertheless this should not preclude a consideration of the meaning of net production.

SOUTHWOOD (1966) states that "net production should include; the increase in standing crop during the season or other time unit; the biomass of all individuals that died or were eaten during the season; the biomass of the total number of exuvaie or other products shed by all the individuals (those alive and now dead); the biomass of any reproductive products, young individuals or adults that have left the area. To be strictly accurate the biomass of any individuals that immigrated into the population should be subtracted and the total amunt of nitrogenous waste estimated".

PETRUSEWICZ (1967) defines net production as 'the tissue produced by the population i. e. the biomass (energy) accounted for by the newly produced organism (Pr) and the weight gains (energy, Pg) of all members of the population i. e. by the weight gain (a) of the organisms of the original standing crop (Bo), (b) of immigrants from the moment they join the population and (c) of the organisms produced in the population during the particular time interval".

PHILLIPSON (1975) defines production as equal to the energy content of the biomass of materials digested during a specified time interval (regardless of whether they all survive to the end of that interval) less that respired or rejected. This definition although quantitatively identical to those of SOUTHWOOD and PETRUSEWICZ, implies that independent measurements of assimilation (A) and respiration (R) are sufficiently accurate to estimate, by difference, production.

The central theme in the direct measurement of production is the measurement of survivorship i. e. the quantification of natality and mortality. This aspect is by far the most complex and requires comprehensive data from field density and age-structure changes, field developmental times and reproductive rates. If all these parameters are satisfactory then an acceptable attempt at obtaining latively few species are technically and biologically amenable to this treatment. Among the oribatids a survivorship curve and subsequently an estimate of production can be made. Unfortunately re- for example, most species appear to possess an almost continuous breeding season, at least judging from the presence of larvae and egg-carrying adults in the field. Subsequently age-structure changes are complicated by overlapping generations which does not permit the classical cohort analysis to be undertaken. In addition larval and nymphal life-stages of oribatid species are inefficiently extracted, possibly in a differential manner, further complicating any estimates of natality and mortality. Faced with this situation an investigator has little alternative but to accept the realities of the data and forego cohort analysis in favour of simpler, but inherently less accurate, methods of estimating net production.

10.2. Methods

10.2.1. *Known biomass changes*

PETRUSEWICZ (1967) defines "total biomass growth (G) as the total organic matter produced in time T, expressed as the sum of all biomass growths (g_i) (all biomass changes having a positive sign) i. e. $G = \sum_{i=1}^{i=k} g_i$". In theory total biomass growth is not normally equal to net production (P) but G = P plus L where L represents the weight losses i. e. that part of the assimilation (A) that enters the population's own tissue and is utilised for the population's own needs in the period of time when respiration (R) is greater than assimilation (A). Total biomass growth is therefore a concept intermediate between production (P) and assimilation (A, gross production.

Although production and total biomass growth are different concepts they are often regarded as equal mainly because of the inadequate accuracy of ecological data (PETRUSEWICZ 1967). Two major assumptions are made when positive biomass increments are used to estimate net production; there were no weight losses (L); there was a complete knowledge of all the actual biomass changes, ($\pm$ AB) in the population. Neither of these assumptions are realistically valid, particularly the second. Biomass changes, both negative and positive, occur simultaneously and even the most intensive sampling programme is unlikely to record them all. Nevertheless positive biomass increments do provide an estimate of net production which can then be used in a comparative manner.

10.2.2. *Mean standing crop and egg (young) mortality*

ENGELMANN (1961) produced an estimate of net production from a consideration of mean standing crop and an estimate of egg (young) mortality based upon the laboratory life history studies of *Oppia nova*.

ENGELMANN assumed an annual turnover of the mean standing crop. Several species initiate and complete more than one generation in a year whereas others may take in excess of twelve months to complete their development from egg to gravid adult. The assumption of a yearly turnover of standing crop will in these cases either under-emphasise or over-emphasise the value of the net production estimate. It becomes necessary therefore to allow for the number of generations initiated each year. It is considered from the age-structure data that *P. punctata* has two generations each year, subsequently the mean monthly standing crop during this period should be doubled. Evidence related to the number of generations produced each year was derived either from the age-structure data of the present study, or from the literature. It is not intended to suggest that generations would be of equal size and for no species or species-group were more than two generations a year assumed. The standing crop of each species or species-group, and the net production estimates obtained from the use of positive biomass increments were converted to energy units using the data from the calorimetry studies.

The number of eggs produced in each year by *P. peltifer*, *N. silvestris* and *H. gibba* was estimated using the method outlined by SAITO (1965). By combining eggs produced and relevant adult mean densities then the egg (young) mortality for these species was calculated. The mean percentage egg mortality from these three species was then used to estimate egg (young) mortality for *P. punctata*, *T. velatus*, *S. magnus* and *S. striculus*. This method is not directly applicable to the species-group, *Nanhermannia* sp., *Oppia-Suctobelba* sp. and "other oribatids" because of the lack of age-structure data and species composition. However where this data is known, i. e. for the five species studied, adults contribute on average 67.2 % to total mean biomass and 32.4 % to total mean numbers. Using these figures then the number of adults and their mean weight can be calculated for each species-group. Once this information was derived it becomes possible to calculate egg (young) mortality for these groups in a manner similar to that used for *P. punctata*.

ENGELMANN (1961) records that an average oribatid egg weighs 3.0 % of adult weight. Using this value, the mean adult dry weights and the calorific value for spittlebug eggs [26.4 kJ (6.3 Kcals) g dwt WIEGERT 1964], the egg (young) mortality was expressed in energy units.

10.2.3. *From known metabolism*

ENGELMANN (1966) and MCNEILL and LAWTON (1970) have derived relationships between production (P) and respiration (R). The information given by MCNEILL and LAWTON is of the greater value both in content and the author's attempt to differentiate between long and short-lived poikilotherms. The latter equations are most relevant to this investigation, i. e.

$$\text{Log R} = 1.1740 \text{ Log P} + 0.1352 \quad \text{---- (1)}$$

$$\text{Log P} = 0.8262 \text{ Log R} - 0.0948 \quad \text{---- (2)}$$

where R and P are expressed in Kcals $m^{-2}yr^{-1}$.

Using the population metabolism estimates calculated previously (Table 9), the production values for each species and species-group calculated using equation 2.

10.3. General remarks

The production estimates obtained from the three methods used are given in Table 14.

Comparison of the estimates from the modified ENGELMANN and PETRUSEWICZ methods, with the exception of *S. magnus* and *S. striculus*, show two contrasting trends. The modified ENGELMANN method gives lower estimates of net production for individual species popula-

Table 14. Estimates of net production (kJ m^{-2} yr^{-1}) using three methods

Species or species group	Modified ENGELMANN		PETRUSEWICZ		McNEILL and LAWTON	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Nothrus silvestris	1.156	1.461	1.457	1.880	1.813	1.980
Platynothrus peltifer	0.657	0.997	1.122	1.193	1.143	1.595
Hermannia gibba	2.374	3.027	3.379	4.815	2.486	3.546
Tectocepheus velatus	0.126	0.151	0.130	0.155	0.373	0.456
Parachipteria punctata	0.833	1.578	0.987	1.336	1.055	1.717
Steganacarus magnus	1.281	1.227	0.917	1.013	0.875	0.871
Steganacarus striculus	0.460	0.494	0.272	0.289	0.582	0.611
Oppia-Suctobelba sp.	0.193	0.176	0.147	0.138	0.707	0.653
Nanhermannia sp.	1.118	0.724	1.319	0.611	1.608	1.248
'other oribatids'	1.369	1.846	1.143	0.967	1.985	2.659
Total Oribatei	**9.567**	**11.681**	**10.873**	**12.379**	**12.627**	**15.336**

Table 15. Energetics data for a field population of oribatid mites (kJ m^{-2} yr^{-1})

Year	C	A	P	R	FU	
1.	94.429	22.772—25.833	9.567—12.627	13.205	51.154	
2.	119.437	28.600—32.255	11.681—15.336	16.919	64.699	
	A/C	P/C	R/C	R/A	P/A	P/R
1.	24.12—27.36	10.13—13.37	13.98	57.99—51.12	42.01—48.88	72.45—95.62
2.	23.95—27.01	9.78—12.84	14.17	59.16—52.45	40.84—47.55	69.04—90.64

tions whereas the reverse is true when the species-groups are considered. When species are grouped into a single category it is probable that the component species will differ with respect to their reproductive period, developmental time and the number and magnitude of generations initiated within each year. If this is true then the biomass changes could be masked resulting in a lower estimate of net production by positive biomass increments. In contrast the more precise density and biomass data collected for individual species populations are likely to reflect more accurately the biomass changes taking place in the field. Indeed the individual species biomass data does tend to show a greater number of positive and negative changes between sampling occasions and that these changes are of greater magnitude than those for species-groups. The use of the mean standing crop reduces the significance of large and frequent biomass changes and therefore the modified ENGELMANN method inherently produces lower estimates of net production for the individual species populations. Additional evidence of this effect is shown by *Nanhermannia* sp. and *P. punctata* where the magnitude of biomass changes is greater in year 1 than in year 2. Consequently the modified ENGELMANN method produces lower estimates of net production in year 1 when compared to the PETRUSEWICZ, method the reverse is true in year 2. A further complication may arise from the assumption that for certain species and species-groups, a maximum of two generations a year were completed. If this assumption is erroneous, and a greater number of generations are completed each year, then the modified ENGELMANN method will underestimate net production. Indeed certain authors have attributed 3 genera-

tions a year to *Oppia quadricarinata* and *Suctobelba subtrigona* (BERTHET 1964, LEBRUN 1964) and up to 5 generations a year to *T. velvatus* (LEBRUN 1964).

The highest estimates of net production for each species and species-group, with the exception of *H. gibba* and *S. magnus* are obtained from the use of the MCNEILL and LAWTON equation. The reasons for these higher values are obscure, but it is noticeable that the peaks of biomass for these populations often coincide either with high field temperatures, (June to September) or with a rise in field temperatures (April to May). This is particularly evident for *N. silvestris* and *P. peltifer*. In contrast the major biomass peaks of *H. gibba* occur in March and December when the field temperatures are relatively low. The net production estimates for this species from the MCNEILL and LAWTON equation are appreciably less than those obtained from positive biomass increments. The timing of biomass peaks together with the established influence of temperature upon respiratory rate is probably sufficient to account for the observed differences between the estimates derived from known metabolism and those obtained from the other methods used.

The highest net production estimates for *S. magnus* were obtained from the modified ENGELMANN method. It is possible that the production afforded to egg mortality was overestimated. In the present study egg weight was estimated as 3.0% of adult dry weight. (ENGELMANN 1961), which gives a value of 4.0 μg for an average adult *S. magnus* of 132.6 μg dry weight, (biomass data Table 2). This method of estimating egg weight may be inaccurate for species similar to *S. magnus* whose adults contain particularly high proportions of inert material. WEBB & ELMES (1972) suggest that the egg of *S. magnus* weighs approximately 2—3 μg dwt. Consequently production due to egg mortality for this species from the present study may have been exaggerated by up to 50%. This could also explain the high estimates for *S. striculus* obtained from the modified ENGELMANN method. Each of the methods employed to assess net production is subject to criticism at a fundamental level. The modified ENGELMANN estimates are partially derived from mean standing crop with an allowance for turnover based upon the adjudged number of generations completed each year. Standing crop is the end product of additive and subtractive processes and therefore is not a direct measure of production. The PERTUSEWICZ method measures the positive changes in standing crop between sampling occasions and is unlikely to be accurate unless the sampling frequency is sufficient to measure all the biomass changes occurring in the field. Indeed HEALEY (1967) considers that estimates derived from positive biomass increments measure "minimum net production" because the method takes no account of the biomass increments that occur to some part of the population cohort at times when their contribution to production is being masked by quantitatively greater mortality elsewhere. The prediction of production from population metabolism can be misleading. The MCNEILL and LAWTON equation for short-lived poikilotherms gives decreasing production/respiration ratios as the value of the population metabolism increases. Consequently if there are large differences in the population metabolism of certain species between years then the use of the MCNEILL and LAWTON equation would suggest that changes in the production/respiration relationship have occurred. However such changes are more likely to be a product of the equation rather than the possibility that proportionately more, or less, energy is being channelled into net production. It is difficult therefore to assess which of the methods used is the most accurate or even whether any of the methods provide estimates which are close to the true net production value. Nevertheless until more precise information relating to field developmental times, natality and mortality rates of oribatids becomes available, it seems likely that indirect methods for the estimation of net production will continue to be of value.

11. Energy budget

The energy budget of the field population of oribatid mites for each year of the study is summarised in Table 15. The estimates for energy consumed are 22.554 Kcals m^{-2} yr^{-1} in year 1 and 28.527 Kcals m^{-2} yr^{-1} in year 2. The energy accounted for by production, respiration and rejecta is 17.657—18.388 Kcals m^{-2} yr^{-1} and 94.429—96.354 kJ (22.284

to 23.157 Kcals) m^{-2} yr^{-1} in year 1 and 2 respectively. Consequently approximately 20 % of the energy consumed is unaccounted for.

Comprehensive energetics data for field populations of this group are very limited. The investigation by ENGELMANN (1961) on the oribatids of an old field community, when compared to the present study, show some striking differences. The production/assimilation (P/A) (40.8—48.9 %), production/respiration (P/R) (69.0—95.6 %) and production/consumption (P/C) (9.8—13.4 %) ratios of the present investigation are at least a factor of two greater than those found by ENGELMANN, i. e. 20.9 %, 21.9 % and 4.2 % respectively. This difference is due almost entirely to the fact that the present study reveals a much higher proportion of assimilated energy being converted to tissue (net production). It is considered that the limited sampling programme of the earlier work precludes an accurate estimate of biomass and biomass changes and consequently net production. Indeed when consumption is derived from assimilation and rejecta (FU) then the P/C ratio, 12.5—16.4 %, further diverges from that of ENGELMANN. Closer values are observed between the studies when the respiration/consumption (R/C) ratios are considered, (14.0—14.2 % as compared to 19.2 %). In essence therefore oribatid mites appear to utilise from 1/5 to 1/7th. of their consumed energy in the cost of maintenance. The assimilation/consumption (A/C) ratios for the two studies are superficially similar (24.0—27.4 % compared to 20.1 %). However when C is calculated from the sum of A and FU then the A/C ratio from the present study rises, ranging from 30.7 to 33.6 %. These higher A/C values compare more favourably with those from laboratory estimates on individual species, (*D. clavipes*, LUXTON 1972; *S. magnus*, WEBB & ELMES 1972; and *C. labyrinthicus*, STEIGEN et al. 1975).

Complete energy budget data from laboratory studies of oribatid mites are also limited. The most comprehensive study is that of WEBB & ELMES (1972) on adult *S. magnus*. This work reveals surprisingly high P/A ratios ranging from 74 % for mature females to 96 % for new recently adult males and females. WEBB & ELMES suggest that the assimilation rate may be inflated. However the present work indicates that the P/A ratios for *S. magnus* are of similar magnitude, ranging from 51.6 to 60.9 %. The more recent evidence therefore suggests that oribatid mites belong to a group of soil detritivores which utilise a relatively high proportion of their assimilated energy for net production. This characteristic has been observed in a minority of detritus feeding animals; *Japonaria laminata armigera* (VERHOEFF) [SAITO 1967]; *Isotoma trispinata* MACGILLIVRAY [TANAKA 1970]; *Tipula excisa* SCHUMMEL [HOFSVANG 1973] and the Diplopoda and slugs of Meathop Wood (HALE IBP MS). The range of P/A values for this group of animals is narrow ranging from 40.8 % (present study) to 49.8 % (SAITO 1967). In contrast the majority of soil detritivores have a lower production to assimilation ratio; *Ligidium japonicum* VERHOEFF [SAITO 1965]; *Armadillidium vulgare* (LATREILLE), *Porcellio scaber* (LATREILLE) and *Ligidium japonicum* (SAITO 1969); Isoptera (WIEGERT 1970); *Pogonomyrmex occidentalis* CRESSON [ROGERS 1972]; *Cognettia sphagnetorum* (VEJDOVSKY) [STANDEN 1973a]; *Trichoniscus pusillus pusillus* BRANDT [STANDEN 1973b]; Nematoda (YEATES 1973, WASILEWSKA 1974); *Cryptopygus antarcticus* WILLEM [TILBROOK 1977]; Diptera (RUSSEL-SMITH IBP MS), and the Lumbricidae, Enchytraeidae and snails (HALE IBP MS). The P/A ratios for this group vary between 7.1 % (ROGERS 1972) and 30.6 % (TILBROOK 1977). LUXTON (in preparation) suggests that those animals with high P/R ratios, and in consequence high P/A values, "comprise those organisms compelled to store energy in body tissues to see them through adverse or non-feeding periods" whereas those with low P/R ratios would contain "animals with an extremely high metabolic rate during a relatively short active season (e. g. ants) or those with a somewhat elevated activity and high assimilation efficiency which continues even during the less element part of the year (e. g. molluscs)".

The relative impact of oribatid mites of Meathop Wood can be assessed by their contribution to overall detritivore energy flow. Utilising the figures given by HALE (IBP MS), their contribution to total detritivore assimilation, production and respiration is 1.12—1.60 %, 3.14—5.03 % and 0.76—0.98 % respectively. Data of MACFAYDEN (1963), KITAZAWA (1971)

and VAN DER DRIFT (1974) confirms that the contribution of oribatids in temperate deciduous woodland systems to total detritivore respiration is of a similar order to (0.68 to 7.49 %). Higher respiratory contributions are observed for oribatids of temperate coniferous forests, 10.5 % (MACFADYEN 1963) to 18.18 % (HUHTA & KOSKENNIEMI 1975) with an extremely large value of 41.48 % (KITAZAWA 1971) for the "Acari" of an equatorial highland forest. The evidence therefore suggests that the role of oribatid mites as measured by their direct contribution to energy flow, in ecosystems comparable to Meathop Wood, is negligible.

If this is true then why do oribatid mites occur in such large numbers in comparable ecosystems? One suggestion is that they play a major role in the fragmentation of dead organic matter which facilitates the leaching of soluble materials and also provides increased surface ares of leaf material for microbial exploitation (LUXTON 1972). BERTHET (1967) estimated that 20 % of annual leaf fall passes through the gut of oribatid populations. The total annual non-woody litter fall at Meathop Wood in 1967 and 1968 was estimated as 767.9 g dwt m^{-2} (SYKES & BUNCE 1970). Overall consumption by the oribatid population, ignoring the presence of different feeding preferences within this group, accounts for only 1.5 % of this figure. Indeed if litter fall is extended to include woody litter then the consumption precentage falls to 1.1 %. There is little evidence therefore from Meathop Wood that the fragmentation of dead organic matter is greatly facilitated by the feeding activities of the oribatid population. The possibility that the oribatids have other indirect effects such as acting as dispersal agents for microbial flora, stimulating senescent fungal colonies by grazing, enhancing successional microfloral attack and conditioning substrates for microbial exploitation have been amply considered by LUXTON (1972 and in prep.) and warrant no further amplification here. MCBRAYER (1977) has shown that soil decomposer invertebrates upon death release substantial quantities of critical elements, particularly nitrogen and phosphorus. The precise role of oribatids in the release of such elements is unknown but it would appear to be small at Meathop Wood when their production and contribution to soil fauna biomass is considered. Exceptions may occur where the oribatid population constitutes a more significant proportion of the soil fauna.

This study reveals a minimal direct contribution to energy flow by oribatid mites. Nevertheless there is a requirement for quantitative data which measures the extent of the interactions between oribatid populations and other soil organisms, particularly the microflora. Once this becomes available only then can a balanced judgement be made of the significance of these organisms in the functioning of ecosystems.

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13. Summary

This investigation was concerned with a study of production and energy flow through a population of oribatid mites from a mixed deciduous woodland. Monthly population density data wer determined for the period August 1967 to July 1969. Seasonal fluctuations in the age-structure composition of five species; *Nothrus silvestris*, *Platynothrus peltifer*, *Tectocepheus velatus*, *Hermannia gibba* and *Parachipteria punctata* are given. The mean monthly biomass, and the maximum and minimum monthly biomass, for each year of the study was determined for the total population and for seven individual species and three species-groups. Calorific values for seven species of oribatid mites and six potential food materials were determined. The respiratory rate at 15 °C was measured for certain juvenile and adult life-stages of *Nothrus silvestris*, *Platynothrus peltifer* and *Hermannia gibba*. Annual population metabolism for each species and species-group was estimated. The influence of temperature upon defaecation rate was investigated, and the assimilation rate of adult *Nothrus silvestris*, *Platynothrus peltifer* and *Hermannia gibba* determined. Estimates of consumption and faecal biomass for the total and individual components of the oribatid population are given. Net production of the oribatid population was determined.

The energy consumed (C) by the total population was estimated as 94.429 and 119,407 kJ (22.554 and 28.527 Kcals) m^{-2} in year 1 and 2 respectively. Net production (P) accounted for 9.567—12.627 kJ (2.285—3.016 Kcals) m^{-2} in year 1 and 11.681—15.336 kJ (2.790—3.663 Kcals) m^{-2} in year 2. Population metabolism (R) was estimated as 13.205 kJ (3.154 Kcals) m^{-2} in year 1 and 16.919 kJ (4.041 Kcals) m^{-2} in year 2. The oribatid population rejected (FU) 51.153 and 64.699 kJ (12.218 and 15.453 Kcals) m^{-2} in year 1 and 2 respectively. Of the energy consumed approximately 20% was unaccounted for by the sum of net production, population metabolism and rejecta. The contribution of the oribatids to energy flow through the detritivore population at Meathop Wood is considered small as the amount of material consumed represents only 1.1% of the annual woody and non-woody litter fall.

14. Literature

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